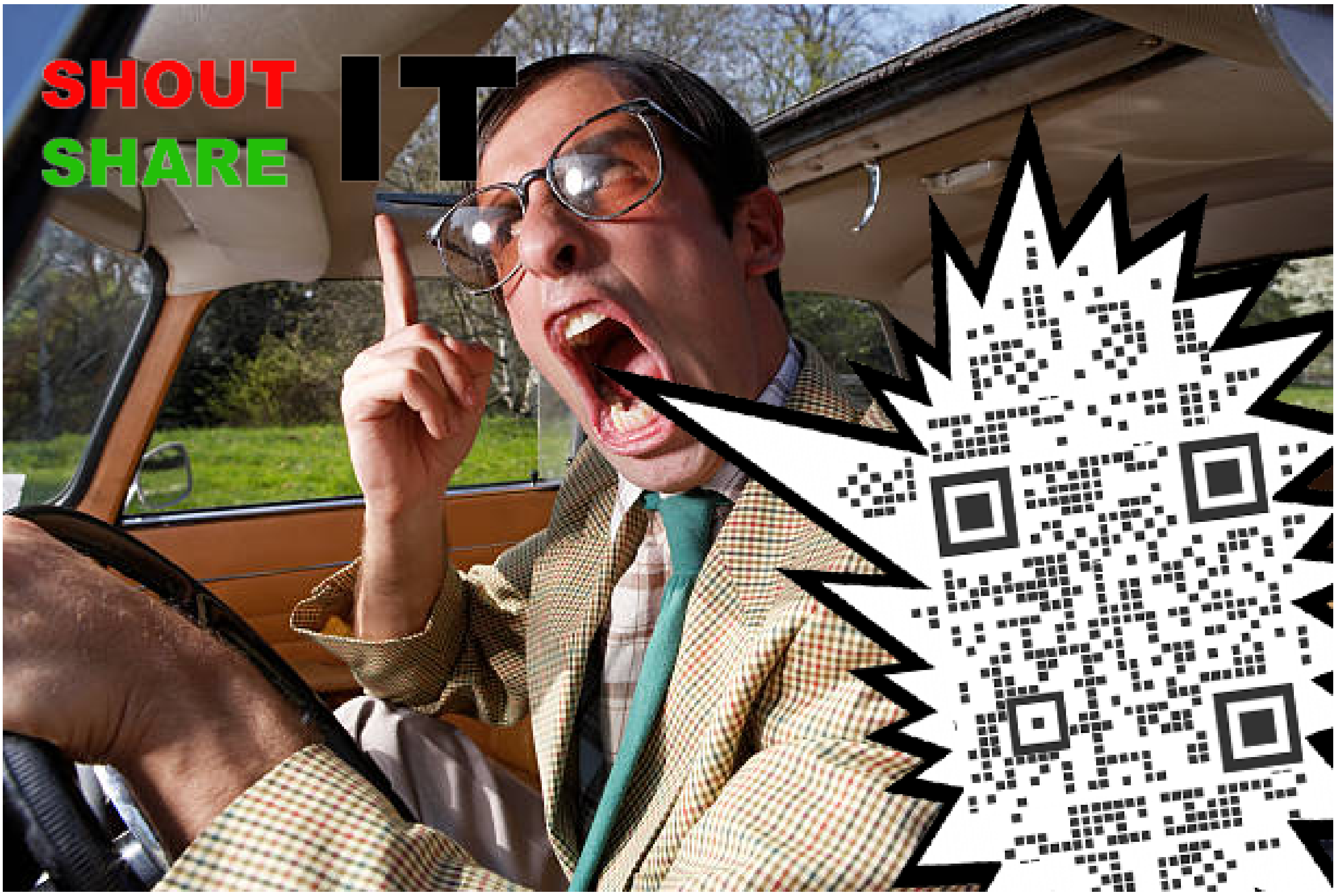
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The lichen genus *Usnea* subgenus *Neuropogon*

F. Joy Walker

Botany series Vol 13 No 1 28 March 1985

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The lichen genus *Usnea* subgenus *Neuropogon*

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Synopsis

A world-wide taxonomic revision is presented for the lichen genus *Usnea* subgenus *Neuropogon*. In summary, this subgenus is here circumscribed to include polar-alpine species with a yellow to yellow-green thallus with varying black or violaceous black pigmentation; a black, or rarely brown, matt apothecial disc, often with excipular rays; and almost always a saxicolous habitat. Fifteen species are recognised, of which three are new: *Usnea patagonica, U. pseudocapillaris*, and *U. subantarctica*. Two described species, *U. durietzii* and *U. neuropogonoides*, are included in the subgenus for the first time; one name change, *U.*

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sulphurea to *U. sphacelata*, has had to be made resulting from nomenclatural considerations; three new combinations are made: *U. acanthella* (Lamb) F. J. Walker, *U. perpusilla* (Lamb) F. J. Walker, and *U. subcapillaris* (D. Galloway) F. J. Walker. Several taxa are reduced to synonymy, including *U. melaxantha* with *U. aurantiaco-atra* and *U. rohmederi* with *U. perpusilla*. The taxonomic section is preceeded by an outline of previous research and accounts are given of morphology, chemistry, distribution, ecology, phytosociology, and biogeography. Reasons for accepting subgeneric status are given. In delimiting species much consideration has been given to the polymorphic nature of *Usnea* species and hence a wide range of infraspecific variation is often tolerated. A detailed account is provided for each species with particular emphasis attached to variation, chemistry, and species concepts. Three allied species belonging to *Usnea* subgenus *Usnea* which may be pigmented are included in the key to the species and are discussed in Appendix I.

Introduction

Previous collections and research

Species of *Usnea* subgenus *Neuropogon* form one of the most conspicuous groups of bipolar-alpine lichens, often being the dominant fruticose lichens found in such inhospitable localities. Apart from a distinctive variegated black and yellow-green colouration (yellow to ochraceous in herbaria) and comparatively large size, members of the group are more easily collected than other associated saxicolous lichens which are frequently crustose. Consequently the group has often formed the major part of collections made by botanists and non-botanists alike on expeditions to the antarctic and arctic from the late eighteenth century to the present day. Despite their prominence there are still certain areas, in particular the northern Andes and even Central and North America, where the subgenus is extremely rare and difficult to interpret. Frequently the only known collections from these areas have been made by explorers and mountaineers, for example Whymper; further field work is needed to fill in the gaps that still exist in distributional patterns and to provide the essential ecological information which is particularly needed for the study of this group.

The first arctic *Neuropogon* specimens to be brought back to Europe by explorers and described as new taxa by contemporary lichenologists were collected during the late eighteenth and early nineteenth centuries. Early literature was restricted to the description of individual species and the first group of these, *Lichen sulphureus* (König, 1772) and *L. pallidus* (Retzius, 1779), were based on material collected in Iceland, whilst *Usnea sphacelata* (Brown, 1823) was described from arctic North America. During the same era expeditions to southernmost areas of South America also brought back *Neuropogon* material. The earliest southern hemisphere species to be described, *Lichen aurantiaco-ater* (Jacquin, 1781), i.e. *Usnea aurantiaco-atra*, was based on collections made by Commerson in 1767 from the Magellan Straits area. Other notable collectors of new taxa during the early nineteenth century include Cavanilles (Acharius, 1803) and Gaudichaud (Persoon, 1828), who both collected on the Falkland Islands, as well as Poeppig (Nees & Flotow, 1835) from southern Chile. Material was also collected by Darwin from Tierra del Fuego in 1833 and in his journal (Darwin, 1979) he likens the abundance of the extensive swards of *Neuropogon* around Cape Horn to a variety of grass when viewed from a distance.

By the early nineteenth century explorers were beginning to survey the antarctic continent. The first *Neuropogon* species, *Usnea fasciata* (= *U. aurantiaco-atra*), to be described as new from Antarctica was brought back to America from the South Shetland Islands (Torrey, 1823), probably by a whaling party. Hooker's account of the botany of the voyage of the ships 'Erebus' and 'Terror' (Hooker, 1844–47) and 'Lichenes antarctici' (Hooker & Taylor, 1844) provided the earliest accounts of antarctic lichens as a group and also recorded the presence of *Neuropogon* species on Îles Kerguelen, one of the isolated subantarctic islands in the southern Indian Ocean. These islands were revisited by other expeditions during the latter part of the nineteenth century, with *Neuropogon* taxa being described from collections made by the 'Venus Transit' Expedition (Crombie, 1876*a*) and the 'Challenger' Expedition (Stirton, 1881). This was not long after the description (Nylander, 1866) of the first Australasian taxon, *Neuropogon melaxanthus* var. *ciliatus* (= *Usnea ciliata*).

Major expeditions to Antarctica on which notable lichen collections were made have been adequately listed by Dodge (1948) for the period 1839–1935 and Lamb (1964) for 1901–1958, together with details of relevant publications and herbaria. Arctic collections have mainly been the province of Scandinavian expeditions and relevant historical collections have been adequately cited by Lynge in various publications (for example: Lynge, 1932, 1941).

Late nineteenth and early twentieth century lichenologists who contributed to the knowledge of the group included Müller (1888, 1895), Du Rietz (1926), Räsänen (1932), and Zahlbruckner (1903, 1917), although many of the taxa described by them were subsequently reduced to synonymy. Howe (1915) produced a useful compilation of type data of South American taxa, whilst Du Rietz (1926) provided the first comparative account of the southern hemisphere species although he excluded relevant chemical information.

The three twentieth century lichenologists that feature most prominently in the study of *Neuropogon* are Motyka, Lamb, and Dodge. These authors produced detailed taxonomic studies that were mainly based on collections made by contemporary antarctic expeditions and surveys. Important collections included those made by members of the British Antarctic Survey, formerly 'Operation Tabarin' prior to 1946, and the Falkland Islands Dependencies Survey (F.I.D.S.) 1946–1961.* Others include the British, Australasian, New Zealand Antarctic Research Expedition 1929–31 (B.A.N.Z.A.R.E.), and the United States Antarctic Service Expedition 1940–41 (U.S.A.S.). Lamb (1948*a*) also studied some of the rich collections made in Patagonia by Santesson from 1939–41 (S, UPS) which have also been invaluable to the present author during this reappraisal of the group.

Motyka (1936–38) included 12 species in the subgenus *Neuropogon* and also described an additional two species in the subgenus *Euusnea* nom. illeg. (Article 21.3), i.e. *Usnea*, that are accepted here as belonging to the group. Motyka was the first author to include any indication of medullary chemistry in his account, which was limited to spot tests with potassium hydroxide solution (K).

The most detailed monographic account was produced by Lamb (1939*a*) who revised Motyka's work and recognised 13 species and their varieties and forms. Lamb was the first author to make a detailed study of medullary chemistry of the group, using thallus spot tests and microchemical crystal tests, and to use this information on a taxonomic basis. Lamb later (1964) had access to some thin-layer chromatographic (TLC) data provided by Hale. This was a major step forward, although sometimes too much weight was attached to minor chemical differences which would today be regarded as individual races, rather than distinct taxa, by most taxonomists. Lamb subsequently (1948*a*, 1964) emended and added to his earlier account, eventually recognising a total of 15 species of *Usnea* subgenus *Neuropogon*. He also realised that many of his individual forms were simply chemical 'phases' of a particular species that were only significant at a distributional and ecological level.

There have been few reports of medullary chemistry of *Neuropogon* besides those of Lamb. These include Hawksworth & Moore (1969), Golubkova & Schapiro (1970), Kashiwadani (1970), Filson (1974), and Ghogomu & Bodo (1982), which frequently report the lack, rather than the presence, of depsidones.

Lamb's work provided a sound basis for the identification of *Neuropogon* species world-wide with particular emphasis on antarctic and some South American taxa. Meanwhile Dodge and associates (Dodge & Baker, 1938; Dodge, 1948, 1965*b*, 1973) had much narrower species concepts and described a series of additional species. Many existing infraspecific taxa were raised to specific rank, often without the study of extant type specimens. Dodge's work was confined to Antarctica and the subantarctic islands of the Indian Ocean in which he recognised 21 species (Dodge, 1973) and six species (Dodge, 1948, 1965*b*) respectively, accepting a grand total of 30 species in *Neuropogon*, including one arctic and two Australasian taxa. Some of the taxa described by Dodge have been examined by Lamb (1964) and tentatively reduced to synonymy. Lamb's interpretations of Dodge's material have, for the most part, been followed here, particularly where type specimens have not been made available for study; many of the species distinguished by Dodge were separated on minute morphological differences with little or no reference to chemical data.

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* The collections made by 'Operation Tabarin' were referred to by Lamb as F.I.D.S. both on herbarium labels and in subsequent publications (Lamb, 1964); both names are used here following label details.

More recent work has primarily concentrated on ecological observations and several plant associations have been described based on *Neuropogon*-containing communities with other lichens and bryophytes. Examples include Smith & Corner (1973), Follmann (1965*a*, 1967), Lamb (1970), and Gimingham & Smith (1970). Taxonomic work has been limited to the preparation of local antarctic and subantarctic floras following Lamb's treatment and includes floras of South Georgia (Lindsay, 1975), the South Orkney Islands (Smith, 1973), the South Sandwich Islands (Longton & Holdgate, 1979), Marion Island (Lindsay, 1977*b*), Macquarie Island (Filson, 1981), Mac. Robertson Land (Filson, 1966, 1975), Wilkes Land (Filson, 1974), and Bouvetøy (Jørgensen, pers. comm.). These floras have been produced in conjunction with recent expeditions or the work of permanent scientific bases (for example, the British Antarctic Survey) that have been established around the antarctic continent by various nations.

The aim of this present study is to give a comprehensive account of the species belonging to *Usnea* subgenus *Neuropogon*. Special emphasis has been placed on the circumscription of the species in the light of the wide range of infraspecific variation, new chemical data, and relationships with closely allied taxa. There has been no critical work on the subgenus since that of Lamb (1939*a*, 1948*a*, 1964).

Taxonomic review

Neuropogon was published as a genus by Nees & Flotow (1835) within the Usneaceae (= Parmeliaceae, Henssen & Jahns, 1973) and was based on two species *N. poeppigii* and *N. antennarius*. *N. poeppigii* was subsequently transferred from the genus by later authors, details of which are given by Lamb (1939*a*, 1964), commencing with the transfer to *Chlorea* by Nylander (1860) and, more recently, to the subgenus (Motyka, 1936–38) or genus *Protousnea* (Krog, 1976). Nylander (1860) is consequently considered to have emended the original concept of the genus since the original description of Nees & Flotow circumscribed both *Protousnea* and *Neuropogon*, based on common features of thallus colour, anatomy, apothecial shape, and disc colour. However the citation '*Neuropogon* (Nees & Flotow) Nyl.' by Lamb (1939*a*) is erroneous as no new combination was actually made by Nylander. Nylander (1860: 272) is also considered to have, in effect, selected *N. antennarius* as the lectotype of *Neuropogon*, consequently Motyka's (1936–38) citation of *N. melaxanthus* as the type species is superfluous.

The genus *Neuropogon* was relegated to the rank of section or subsection of the genus *Usnea* Hill ex Browne (Laundon, 1984) by Montagne, in Gay (1852), and to a subgenus by Jatta (1900), although he (Jatta, 1909) later accepted *Neuropogon* as a distinct genus. Jatta's combination (Jatta, 1900) *Usnea* subgenus *Neuropogon* (Nees & Flotow) Jatta was based on two species, *Usnea arboricola* and *U. soleirolii*, that were not subsequently regarded as belonging to the subgenus and were finally included in *Lethariella* subgenus *Lethariella* (Krog, 1976). For this reason Jatta's combination was wrongly regarded as invalid by Motyka (1936–38) and omitted by Lamb (1964). However, in accordance with the Code (Article 63.2) the combination must be accepted, as the type of *Neuropogon* is, by implication, included in the combination. Consequently the full citation at subgeneric level is *Usnea* subgenus *Neuropogon* (Nees & Flotow, emend. Nyl.) Jatta, and the citation '*Usnea* subgenus *Neuropogon* (Nees & Flotow) Motyka' (Motyka, 1936) is incorrect (Culberson, 1966).

Materials and methods

The following account is based primarily on collections in institutional herbaria. I have also had access to material collected in recent years by the following botanists: James (Patagonia, New Zealand), Henssen & Vobis (Patagonia), Follmann (South America), Santesson (Patagonia), Hertel (Marion and Prince Edward Islands), Engelskjøn (Bouvetøy), Galloway (New Zealand), Bratt (Tasmania), Sømme, Angard (Dronning Maud Land), Seppelt (Knox Coast, McDonald and Macquarie Islands), Halls (Bolivia), and, in addition, extensive collections made by various members of the British Antarctic Survey (Antarctic peninsula and islands).

The material referred to in this study has been subjected to thin-layer chromatography (TLC) by means of standard methods (Culberson, 1972; Culberson & Johnson, 1976; Culberson et al., 1981; Walker & James, 1980). Type specimens have been examined and tested by TLC unless otherwise stated. In the text ± denotes sporadic or low concentration of a given substance. Details of morphology and anatomy were also studied using the scanning electron microscope (SEM) (Cambridge Stereoscan ISI 60A).

Species descriptions are based on either type material or characteristic specimens in rare instances where the type is very atypical. Details of variation, species concept, chemistry and distribution are given for each species, together with notes on typification and nomenclature when applicable. Allied taxa, not considered to belong to *Usnea* subgenus *Neuropogon*, are given in Appendix I, and excluded taxa in Appendix II.

Only selected records are cited for the commoner and more widespread species according to chemical race. Full lists are only given in instances where new records or critical or new taxa are involved.

Author abbreviations follow guidelines laid down by Laundon (1979).

Results

Morphology

For convenience various morphological features are discussed under subheadings. Emphasis is placed on those features that were found to be of value for species delimitation within the subgenus. Species may be divided initially into two groups, namely those which produce apothecia and lack vegetative propagules, and those which produce soredia, pseudoisidia, or isidia and only rarely produce apothecia. Habit and mode of branching, surface ornamentation, and branch anatomy are important diagnostic characters, whilst others, including pigmentation and faveolation were found to be less reliable. The relative importance of these characters is discussed below. It is important to emphasise that within any given species specimens may exhibit considerable variation due to modification by ecological factors (Filson, 1982; Hawksworth, 1973) and consequently certain features may then be atypical of the species. Scanning electron microscopy was used in certain instances to clarify interpretation of some features, for example vegetative propagules, and to show similarities to *Usnea* subgenus *Usnea*.

Habit and mode of branching: Most species within the subgenus can be distinguished by their saxicolous habitat with erect, cartilagineous main branches arising from either a delimited or proliferating holdfast. In some species the form and blackening of the holdfast, together with the initial branching pattern, are characteristic, whilst in other species this is a much more variable feature. For example, *Usnea ciliata* arises monopodially from a proliferating, often blackened, holdfast; *U. durietzii* branches a short distance above a solitary holdfast to give a tree-like habit; whilst in *U. acromelana* and *U. sphacelata* the form is much more variable, ranging from a delimited holdfast to a spreading colonial form.

Occasionally thalli are subpendulous or subdecumbent. This is a feature of *Usnea subcapillaris* and, to a lesser extent, *U. pseudocapillaris*. Many antarctic species may atypically become subdecumbent when growing in very exposed habitats. Similarly, thalli, for example in *U. aurantiaco-atra*, may rarely become detached and develop a scrambling habit resembling that of *U. neuropogonoides*.

The extent of branching in any given species is often very variable although the overall form is often characteristic. Some species remain virtually monopodial or more or less subdichotomous towards the apices, for example *Usnea ciliata* and *U. taylorii*. Others, for example *U. antarctica* and *U. aurantiaco-atra*, may be richly branched from a delimited holdfast. An angular, divergent, branching pattern is characteristic of *U. subcapillaris* and *U. pseudocapillaris* which both branch repeatedly from a confined holdfast to form a loosely interwoven network of fine branches. These two species are further characterised by the very friable nature of the secondary branches, the brittleness is accentuated in herbarium material.

Pigmentation: The extent of black or violaceous black pigmentation of the thallus is very variable within the subgenus and frequently appears to reflect particular ecological parameters (see p. 25). Pigmentation may be extensive or confined to apices or papillae. Pigmentation of the thallus base near the holdfast was rarely of value, owing to the lack of correlation with other features, although it was occasionally used. Although pigmentation is one of the main features of the subgenus it is not unique within *Usnea s. lat.* and its relative importance is discussed elsewhere under 'Generic concept' (p. 42).

Black pigmentation of the apothecial disc is characteristic of most species, although there are two exceptions, *Usnea trachycarpa* and the rarely fertile *U. subantarctica*, which have a brown to rufous brown disc. Pigmentation may also be a feature of vegetative propagules and is only found when soredia or other structures, such as isidia and pseudoisidia, are partially corticate.

Some specimens of the norstictic-salazinic race of *Usnea aurantiaco-atra* assume a pinkish colouration of the medulla in the herbarium. This has no taxonomic value and is not compatible with the pigment found in some *Usnea* species, as for example in *U. roseola*, as reported by Swinscow & Krog (1979).

Surface ornamentation: Surface features may either be uniform or rather variable within the individual species. A smooth, waxy, rarely subfaveolate, thallus with blackened annulations is a constant feature of all four species belonging to the *Usnea ciliata* complex (*U. acromelana, U. ciliata, U. pseudocapillaris* and *U. subcapillaris*). Such annulations may sometimes occur in other species, for example, *U. patagonica*, or may atypically, be the result of weathering effects or necrosis in species where they are usually absent. A smooth, waxy surface is also characteristic of *U. taylorii* which, in addition, sometimes has scattered, slightly raised, pale maculae, formed by protrusion of the axis towards the surface through the cortex. In some species, for example *U. perpusilla* and *U. sphacelata*, the surface is more variable, and may either be smooth and waxy or become more or less scabrid to subpapillate with minute, frequently pigmented, papillae. On occasions this variation may be observed in different parts of the same specimen.

In those species which have a very lax medulla, the primary branches may become notably inflated and attenuated at the point of attachment. This is a particular feature of *Usnea durietzii* and abnormal forms of *U. sphacelata*.

In contrast to *Usnea s. str.*, pseudocyphellae, as described by Swinscow & Krog (1979), do not occur in the subgenus, although they may be recognised when associated with certain forms of asexual propagule formation (see below); the use of the term 'soralium' in the broad sense is preferred in this context. Gaps in the cortex left on the branch after the breaking away of fibrils or erosion of pseudoisidia may sometimes resemble pseudocyphellae.

Papillae: These are recognised as small hemispherical or conical protuberances composed mainly of cortex (Swinscow & Krog, 1979). Prominent papillae are a feature of several species, in particular *Usnea antarctica* and *U. aurantiaco-atra* and, to a lesser extent, *U. subantarctica* and *U. trachycarpa*. In these species the thallus usually lacks the waxy lustre that is a characteristic feature of epapillate species. The relative size and presence of pigmentation of papillae may sometimes be used as an additional distinguishing feature. For example, papillae are small and normally pigmented in *U. sphacelata* and usually coarser and generally lack pigment in *U. antarctica* and *U. aurantiaco-atra*. *U. aurantiaco-atra* has a very varied range of morphology which varies from almost smooth or faveolate to papillate or verrucose-rugose; variation of this diversity may rarely be observed in a single thallus of this species.

Fibrils: Fibrils are regarded (Swinscow & Krog, 1979) as laterally developed appendages containing an axis as well as a medulla. Numerous stout, elongate fibrils on the main branches, derived from papillae, are a feature of *Usnea trachycarpa* imparting a bottle brush-type of appearance; in some individuals the surface in this species may, less typically, be more or less papillate or faveolate. Short, capillaceous, spreading fibrils are often a feature of *U. subantarctica*, whilst in *U. patagonica* the fibrils are usually replaced by extended, thin, rarely branching, lateral branches that bear soralia.

Internal structure: Relative widths of cortex, medulla, and axis are important taxonomic features and are frequently expressed as a ratio. However, a wide range of variation may be exhibited in individual species and, in some instances (Swinscow & Krog, 1979), may be of little taxonomic significance. It is essential to examine well-developed main branches since the medulla may not be fully expanded in finer, secondary branches. Within *Neuropogon* the basic delimitation of the cortex, medulla, and central axis is uniform in all species except *Usnea taylorii*, where a broad axis is deeply invaded by strands of medullary tissue containing algal cells, often resulting in the unique formation of several separate axial strands in this species.

In some species the presence of a lax, arachnoid medulla accompanied by a thin axis, often occupying less than half the diameter in main branches, is diagnostic and occurs in, for example, *Usnea acanthella, U. durietzii, U. perpusilla,* and *U. sphacelata*. In the latter two species there is considerable variation, and the medulla may only be slightly lax and the axis consequently occupying a greater portion of the main branch diameter. By contrast, a compact medulla with a broad axis is a characteristic feature of *U. antarctica* and *U. aurantiaco-atra*. In other species, for example *U. trachycarpa*, although the medulla may sometimes be relatively broad, it is often sublax, and even species which normally have a compact medulla, for example in the *U. ciliata* complex, there may occasionally be some degree of laxness, especially towards the axis. Examples of various transverse sections are given in Fig. 1.

SEM work has revealed that some species with a lax medulla, for example *Usnea acanthella, U. perpusilla*, and *U. trachycarpa*, have medullary hyphae ornamented with small nodular outgrowths. This was not found to be of taxonomic value and has previously been reported in *Usnea s. str.* (López-Figueras & Palacios-Prü, 1981) and also within the Parmeliaceae in *Alectoria s. lat.* (Brodo & Hawksworth, 1977).

Apothecia: Within the subgenus six species: *Usnea aurantiaco-atra, U. ciliata, U. perpusilla, U. subcapillaris, U. taylorii,* and *U. trachycarpa,* produce abundant apothecia and lack vegetative propagules and, to date, four asexual species: *U. acromelana, U. antarctica, U. pseudocapillaris,* and *U. subantarctica* are occasionally fertile. Apothecia have not been observed in the remaining five species: *U. acanthella, U. durietzii, U. neuropogonoides, U. patagonica,* and *U. sphacelata*. The position as well as the form of the apothecium may be a useful diagnostic feature in some instances. For example, in *Usnea subcapillaris* apothecia are lateral, whilst in *U. taylorii, U. trachycarpa, U. aurantiaco-atra,* and *U. ciliata* they are almost invariably subterminal, sometimes with a short, geniculate appendage; in *U. perpusilla* they are often produced laterally in series along a branch, each with a broad area of attachment (Fig. 2). Exceptions to this arrangement frequently occur in all these species.

Excipular rays always occur in *Usnea trachycarpa, U. ciliata*, and *U. subcapillaris* but are only rarely present in *U. perpusilla* and *U. aurantiaco-atra*; they are absent in *U. taylorii*. The undersurface ornamentation of the excipulum may be diagnostic and usually reflects that of the subtending branch. However, in *U. perpusilla* and, occasionally, in *U. ciliata*, the surface may become individually faveolate. The dark disc colour is also a characteristic of the subgenus, although sometimes pigmentation may not be fully developed in abnormal or immature apothecia in those species which normally have a black disc resulting in a greenish grey colouration. *U. trachycarpa* and *U. subantarctica* are unique in the subgenus in having a rufous brown disc.

The spores are similar to those in *Usnea s. str.* and are simple, ellipsoid, hyaline and usually fall within the range 7–10(–12) × 5–7(–8) μm. Variation in size has not been studied statistically, but there appears to be little variation between species and no taxonomic importance has consequently been attached to them here. The structure of the ascus apex is identical to that of the subgenus *Usnea* and corresponds to the '*Lecanora*-type' described by Honegger (1978).

Vegetative propagules: Three types of vegetative propagules are found within the subgenus: soredia, pseudoisidia, and isidia. Soredia are defined as clusters of fungal hyphae and algal cells without cortex, whilst pseudoisidia, which originate in the same way, are outgrowths from

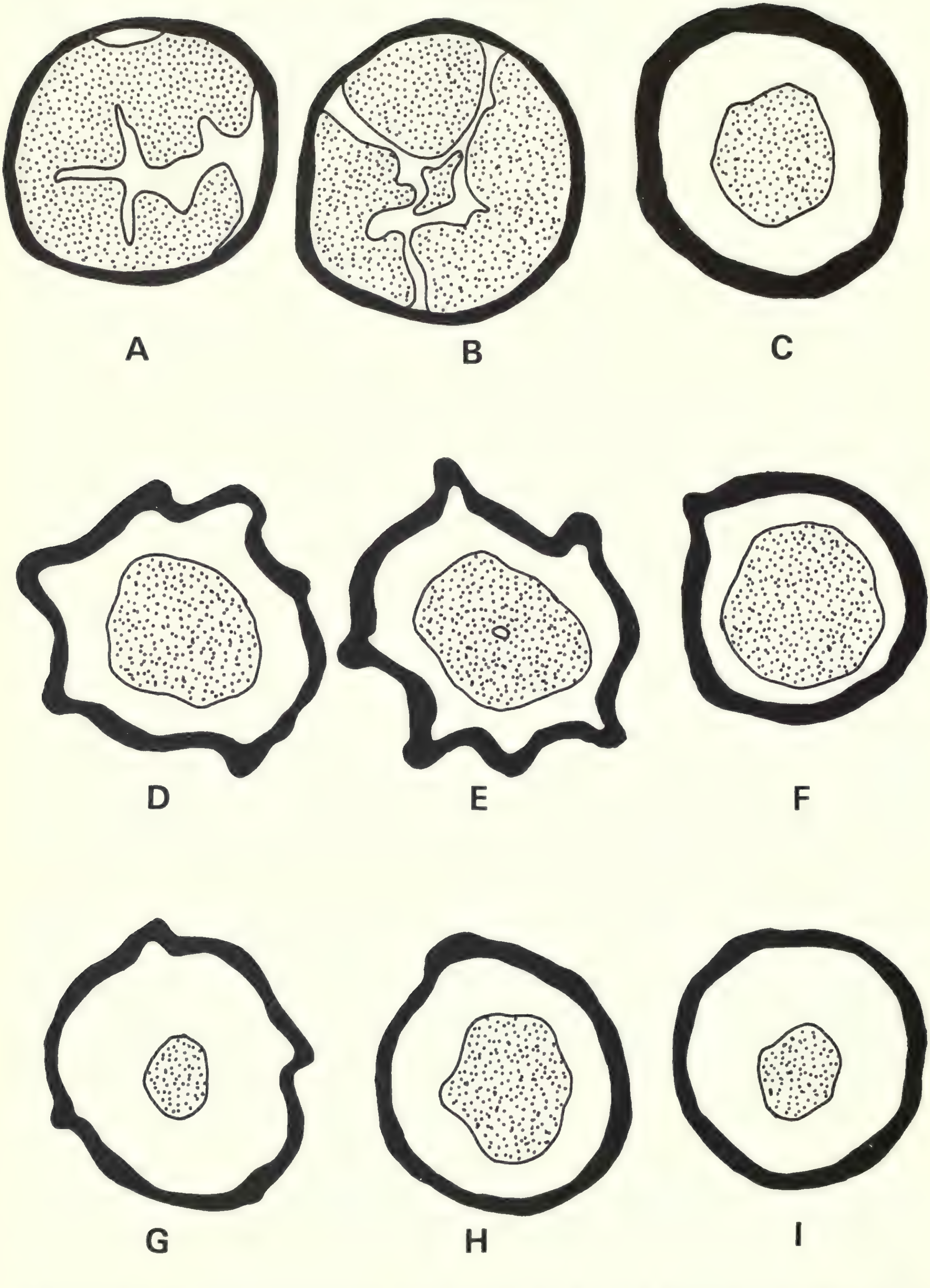

Fig. 1 Examples of transverse sections of main branches. A & B – *U. taylorii,* C – *U. ciliata,* D – *U. antarctica,* E & F – *U. aurantiaco-atra,* G – *U. sphacelata,* H – *U. patagonica,* I – *U. perpusilla.*

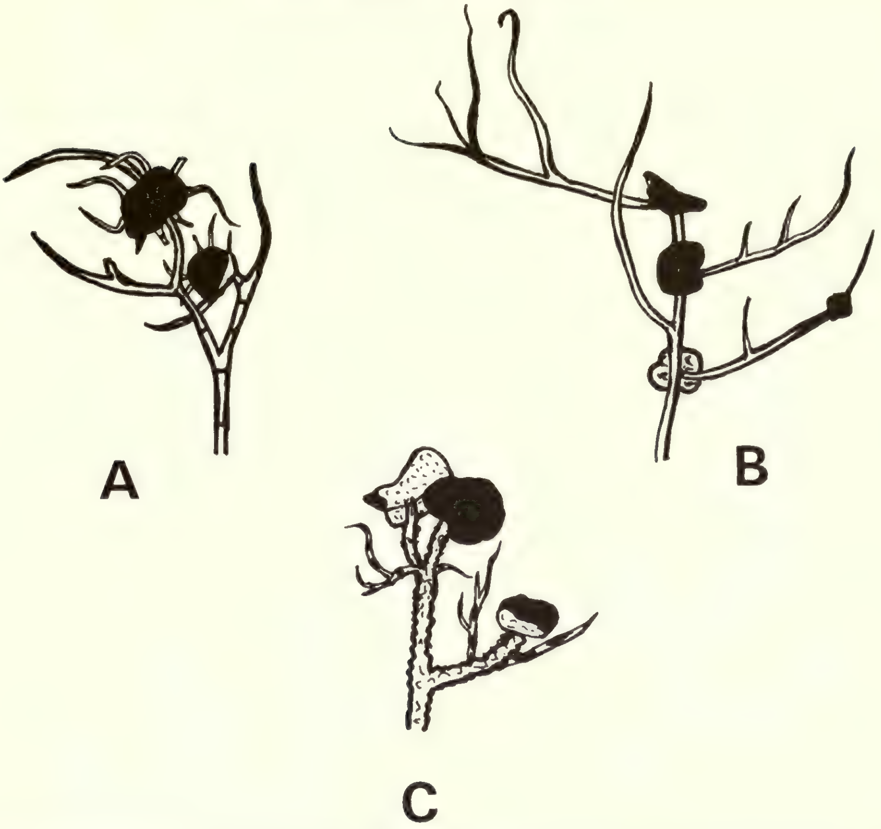

Fig. 2 Disposition of apothecia. A – *U. ciliata* (*Bartlett* 25962, BM) ×2, B – *U. perpusilla* (*Lamb* 6046, CANL) ×4, C – *U. aurantiaco-atra* (*Lamb* 1085, CANL) ×2.

soredia or soralia-like areas that become partially secondarily corticate in contrast to true isidia, which are corticate from conception.

A detailed study of propagules and their formation has been provided by Beltman (1978) using the SEM; similarities with her findings occur in *Neuropogon* species. However, in some instances the clear distinction between soredia, pseudoisidia, and true isidia may be rather difficult to resolve since intergradation and regeneration often occurs. Such intergradation may occur within a species or an individual thallus and is the result of breakdown of the primary propagule, for example pseudoisidia, with the subsequent formation of the second, for example soredia. However, the primary type of propagule formed is specific for the species and consequently used as the diagnostic character. Examination of a range of structures using the SEM has shown that soredia are not corticate, whilst pseudoisidia often have a thin, incomplete, secondarily developed outer cortex, and true isidia have a primary, structured cortex. Differences between vegetative propagules in selected species are given in Fig. 3.

(a) *Soredia:* Shape and formation of soralia in *Usnea*, together with the type of soredia produced, can be diagnostic, although considerable variation may occur within a given species. According to previous investigations (Krog et al., 1980; Swinscow & Krog, 1975, 1979) soralia formation in *Usnea* is either primary or secondary. Primary soralia in, for example, *U. glabratula*, develop directly from the cortex by local breakdown and are usually plane or concave initially, sometimes becoming protuberant on development. Secondary soralia arise from pseudocyphellae subsequent to the breakdown of isidia, for example in *U. subfloridana*, and are often protuberant. However, in this species it is apparent that such soralia may become

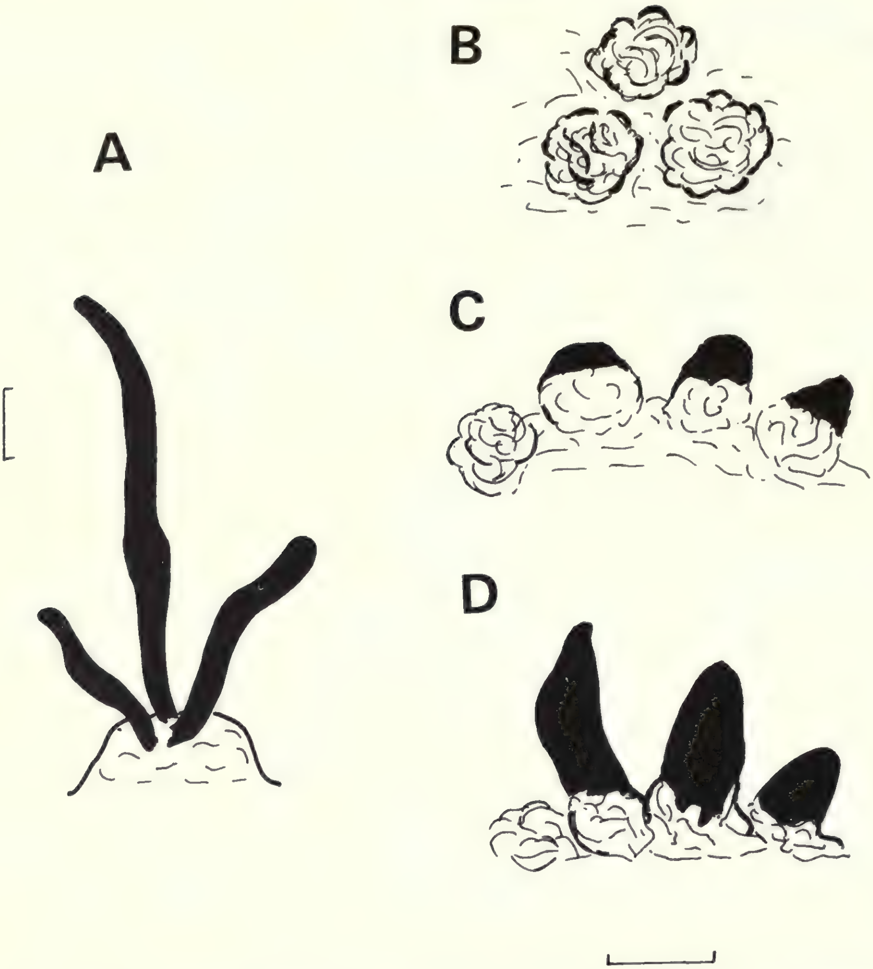

Fig. 3 Vegetative propagules. A isidia – *U. acanthella* (holotype, BM), B soredia – *U. antarctica* (F.I.D.S. B1119, BM), C pseudoisidia – *U. patagonica* (*Henssen & Vobis* 244991, MB), D pseudoisidia – *U. durietzii* (*Gibby & Barrett*, July 1979, BM). Based on SEM studies; blackened areas represent cortex. Scales A = 1 mm, B–D = 50 μm.

corticate, thus producing pseudoisidia. This is in contrast to true isidia that are produced directly from the cortex.

According to the above definition, soralia initiation in the majority of asexual species of *Neuropogon* may be classified as primary, although this distinction is often difficult to interpret in species that produce pseudoisidia. In most species such primary soralia arise directly from the thallus, for example in *Usnea acromelana, U. pseudocapillaris, U. sphacelata,* and *U. subantarctica,* and are initially concave, though they may become convex to globose. Soredia may become secondarily corticate, often very irregularly or thinly so, thus forming minute, more or less spherical pseudoisidia. This is a feature of species which appear to have pigmented soredia; for example in certain forms of *U. acromelana* and *U. sphacelata*, where the pigment corresponds to overlying fragments of cortex. Such structures can be distinguished by size from the cylindrical, more or less elongate pseudoisidia that are a feature of *U. durietzii* and *U. patagonica*.

Soralia initiation in *Usnea antarctica* is unusual and may be classified as secondary in a different sense since they are produced on papillae and, unlike species in which soralia develop from the cortex, are not confined to apices or secondary branches. These soralia often have a distinct crateriform margin and rarely also produce small, dark, pigmented pseudoisidia.

Soredia development in *Usnea patagonica* and *U. durietzii* may also be regarded as secondary since they are produced from the breakdown of pseudoisidia. This process appears to be cyclic since both structures may occur in an individual 'soralium'. In *U. patagonica* such soralia often arise from small papillae but do not have a distinct margin characteristic of *U. antarctica*.

(b) *Pseudoisidia:* Pseudoisidia were defined by Dahl & Krog (1972) as isidia-like structures lacking a true original cortex, such as occur in *Evernia prunastri*. Beltman (1978) found the delimitation impractical in that species, although she observed intermediate structures amongst soralia and lobules that presumably corresponded to pseudoisidia. Other terms have been used to describe similar structures: 'soredial isidia' was used by Du Reitz (1924) and Maas Geesteranus (1947) to describe isidia-like structures formed in soralia to distinguish them from 'isidial soralia' or 'sorediose isidia' (Beltman, 1978) which are produced by breakdown of apices of isidia, as in *Parmelia subaurifera*. Similar small, corticate structures resembling isidia, particularly in *Alectoria*, have been referred to as 'soredialästen' (Henssen & Jahns, 1973); 'isidioid spinules' (Brodo & Hawksworth, 1977) and 'isidial soralia' (Jahns, 1980; Krog et al., 1980).

All these terms appear to correspond to a structure that is characteristic of two species of *Neuropogon*, namely *Usnea durietzii* and *U. patagonica*. The term pseudoisidia is here preferred to describe the small, partially secondarily corticate, pigmented structures that are produced in soralia-like clusters and have the same origin as soralia. The cortex is often ill-defined unlike that found in true isidia. Pseudoisidia are either produced in delimited, soralia-like structures, or may be of secondary origin, formed by regeneration after the breakdown of true isidia as, for example, in *U. torulosa* and *U. amblyoclada* (see Appendix I) where they may also erode to produce soralia.

(c) *Isidia:* True isidia only occur in one species, *Usnea acanthella*, where they may be up to 1 mm in length. They arise as small clusters from tubercules on the surface of the thallus. Such isidia lack a central axis but have a true primary cortex, often with a minute fracture at the constricted base assumed to assist in dispersal, and fracture leaving a scar (Beltman, 1978; Du Rietz, 1924; Maas Geesteranus, 1947). Sometimes fibrillae are also produced in this and other species and may be distinguished by the presence of a central axis; they correspond to structures occasionally observed in *Protousnea dusenii* (Krog, 1976).

Pycnidia: Pycnidia are immersed in the cortex and form irregular, hemispherical swellings, ranging from 100–200 μm in diameter, towards the apices of ultimate branches in pigmented or unpigmented areas. Individual loculi are separated by thallus tissue although often superficially appearing to be compound with several ostioles. Lindsay (1859) provided a detailed account of the pycnidia of *Usnea taylorii* and *U. aurantiaco-atra* (as *Neuropogon melaxanthus*). Lamb (1939*a*) also observed pycnidia in *U. aurantiaco-atra*, and described the conidia as 'staff-shaped, sometimes with a slight eccentric swelling', and subsequently (Lamb, 1948*a*) described those of *U. perpusilla* (as *U. rohmederi*) as 'broadly fusiform'.

Pycnidia are rare and difficult to observe, but have been examined in the following fertile species: *Usnea aurantiaco-atra, U. perpusilla, U. taylorii*, and *U. trachycarpa*. Examination of the type of *U. trachycarpa* f. *elatior* revealed the pycnidial wall to be hyaline whilst in *U. aurantiaco-atra* this was found to be pigmented throughout. More specimens should be examined before any conclusions may be reached, although this might indicate an additional taxonomic difference between species with rufous brown and black apothecial discs.

Conidia were found to be of a similar size in all species, in the range 9–11(–14) × 1–1·7(–2) μm. Their shape conforms to sublageniform as described by Krog (1982) or are more or less narrowly fusiform but are slightly swollen at the proximal end. However, insufficient specimens have been examined to indicate the full range of infraspecific variation. There is apparently no conidial difference between the two races of *Usnea aurantiaco-atra*, at least from examination of the lectotypes of *Neuropogon antennarius* and *Lichen aurantiaco-ater*, both from subantarctic South America.

Krog & Swinscow (1981) described conidial formation in the Parmeliaceae as endobasidial on conidiophores of the bayonet type. The terms 'endobasidial' and 'exobasidial' of Steiner (1901) have often been misinterpreted or confused by previous authors (Lamb, 1939*a*, 1948*a*; Rogers, 1981) when applied to the subgenus *Neuropogon*. These terms have since been rejected by mycologists (Henssen & Jahns, 1973; Vobis & Hawksworth, 1981) and replaced by 'terminal' and 'lateral' as defined by Vobis (1980), each comprising a range of types of conidiophores. The conidiophores appear to correspond to type VI of Vobis & Hawksworth (1981) in which conidiogenous cells arise in branched chains with the conidia arising laterally. However, intermixed with these, some more or less conidiogenous cells are seen to arise directly from the wall tissue (type II); such cells are occasionally seen with one or two percurrent proliferations. In addition, a few conidiophores approximating to type V have been observed in which conidia are produced terminally.

Chemistry

Usnic acid is present in varying concentrations in the cortex of all species. A limited range of *β*-orcinol depsidones (connorstictic, fumarprotocetraric, norstictic, protocetraric, psoromic, 2′-O-demethylpsoromic, and salazinic acids), rarely *β*-orcinol depsides (squamatic and hypothamnolic acids), or fatty acids (murolic acid complex) occur in the subgenus. As in *Usnea* subgenus *Usnea*, frequently a particular species may exhibit more than one chemical race with either different, but often biosynthetically related, substances present. Many species also have an acid-deficient phase which may be dominant, for example, in *U. taylorii* and *U. sphacelata*; one species, *U. acanthella*, has no demonstrable chemistry.

The substances, with the species in which they occur, are given in Table 1. Only those of a diagnostic value are given, whilst substances which may occur in conjunction with one of the main compounds, such as connorstictic acid, cph-1 (yellow accessory with fumarprotocetraric acid, Culberson et al., 1981) and unknown accessory substances, are omitted from the table.

In some species the overall distribution and abundance of certain chemical races may vary but in areas where there is an overlap of two races thalli are encountered which have a composite chemical complement. This phenomenon is known to occur, for example, in *Usnea aurantiaco-atra* and *U. subcapillaris* and often produces evidence against accepting species based solely on chemical differences. Such mixed strains are omitted from Table 1 and are discussed further under 'Circumscription of the species' (p. 39) and *U. aurantiaco-atra* (p. 71).

1. *β-orcinol depsides:* Squamatic and hypothamnolic acids are the only two *β*-orcinol depsides known within the subgenus *Neuropogon*, occurring with, or rarely replacing, *β*-orcinol depsidones in a single species, *Usnea subcapillaris*. This is in contrast to the subgenus *Usnea* where a wide range of depsides is found. Consequently, in specific instances, the detection of *β*-orcinol depsides can be a useful factor in separating certain species of the subgenus from closely allied taxa. For example, in the *Usnea ciliata* complex, squamatic acid is only known in a rare race of *U. subcapillaris* whilst it is frequently found in *U. torulosa*; a species belonging to the subgenus *Usnea* which is superficially similar to some ecotypes of *U. acromelana*. Conversely barbatic acid is sometimes found in *U. torulosa* but has not yet been found in any *Neuropogon* species. Further, in South American collections, the presence of the orcinol depside divaricatic acid in species of *Protousnea* is an additional character useful for separating members of that genus from *Usnea neuropogonoides* or decumbent forms of *U. aurantiaco-atra*.

2. *β-orcinol depsidones:* The range of *β*-orcinol depsidones found in the subgenus *Neuropogon* and related taxa were identified by TLC using solvent systems HEF and TDA following the method of Walker & James (1980). Solvent system G (toluene/ethylacetate/formic acid) of Culberson et al. (1981) was used to confirm the presence of salazinic acid and connorstictic acid in norstictic-salazinic acid chemotypes, using *Parmelia sulcata* and *P. perforata* as controls. The presence of connorstictic acid was only demonstrated when the concentration of norstictic acid was high. Stictic acid has not been found in the subgenus. An additional unknown yellow spot, Rf class TDA 1, HEF 2-3, accessory to norstictic acid, was sometimes found in *Usnea trachycarpa*.

Table 1 Chemical properties of *Usnea* subgenus *Neuropogon*.

		nor	sal	pc	fpc	pso	sqm	hth	fat	frequency
U. acanthella		.	.	.	.	.	.	.	.	.
U. acromelana	1	×	×	±	.	.	.	.	.	C
U. acromelana	2	.	.	.	.	×	.	.	.	R
U. acromelana	3	.	.	.	.	.	.	.	.	L
U. antarctica	1	.	.	±	×	.	.	.	.	C
U. antarctica	2	×	×	.	.	.	.	.	.	R
U. antarctica	3	.	.	.	.	.	.	.	.	C
U. aurantiaco-atra	1	.	.	±	×	.	.	.	.	C
U. aurantiaco-atra	2	×	×	±	.	.	.	.	.	L
U. aurantiaco-atra	3	.	.	.	.	.	.	.	.	C
U. ciliata		×	×	±	.	.	.	.	.	.
U. durietzii	1	×	×	.	.	.	.	.	.	C
U. durietzii	2	.	.	.	.	.	.	.	.	R
U. neuropogonoides	1	.	.	.	.	×	.	.	±	C
U. neuropogonoides	2	.	.	.	.	.	.	.	±	C
U. patagonica		.	.	.	.	.	.	.	+	.
U. perpusilla	1	.	.	.	.	×	.	.	.	R
U. perpusilla	2	.	.	.	.	.	.	.	.	C
U. pseudocapillaris		×	×	±	.	.	.	.	.	.
U. sphacelata	1	.	.	.	.	×	.	.	.	R
U. sphacelata	2	.	.	.	.	.	.	.	.	C
U. subantarctica	1	×	±	.	.	.	.	.	.	C
U. subantarctica	2	.	.	.	.	.	.	.	.	C
U. subcapillaris	1	×	×	±	.	.	.	.	.	C
U. subcapillaris	2	.	.	.	.	.	×	±	.	R
U. subcapillaris	3	.	.	.	.	×	.	.	.	R
U. taylorii	1	.	.	.	±	.	.	.	.	R
U. taylorii	2	.	.	.	.	.	.	.	.	C
U. trachycarpa	1	×	×	±	.	.	.	.	+	C
U. trachycarpa	2	.	.	.	.	×	.	.	+	R
U. trachycarpa	3	.	.	.	.	.	.	.	+	C

Only substances of diagnostic importance are included. nor = norstictic acid, sal = salazinic acid, pc = protocetraric acid, fpc = fumarprotocetraric acid, pso = psoromic acid (including 2′-O-demethylpsoromic acid), sqm = squamatic acid, hth = hypothamnolic acid, fat = fatty acids. Symbols: × = constant; ± usually present as an accessory substance or occurring in low concentrations; + = present in most specimens.
C = Common, widespread throughout range.
R = Rare throughout range or from a single locality.
L = Locally abundant, restricted distribution within range.

Solvent system G was also particularly useful for identification of substances belonging to the fumarprotocetraric acid complex in *Usnea aurantiaco-atra* and *U. antarctica*. The substance cph-1 (Culberson et al., 1981) was frequently found as an accessory substance to fumarprotocetraric acid, producing a yellow spot on developed chromatograms. Its presence was confirmed using *Cetraria straminea* as a control and further by two-dimensional chromatography employing first solvent system G and then HEF, with suitable controls and following fig. 2 of Culberson et al. (1981). This method was also used to confirm the occasional presence of traces of salazinic acid and distinguish it from cph-2 (Culberson et al., 1981), in specimens containing the fumarprotocetraric acid complex. For example, traces of salazinic acid were confirmed in a collection of *Usnea antarctica* from South Georgia (*Lindsay* 4327, AAS) and in *U. aurantiaco-atra* from Tierra del Fuego (*Henssen & Vobis* 24417a, MB), both containing fumarprotocetraric acid as the primary constituent. In the subgenus *Usnea* Swinscow & Krog (1979) found that although protocetraric acid nearly always excluded the production of salazinic acid it nevertheless occurred in some thalli that contained both substances. In *Neuropogon* protocetraric and salazinic acid may occur together when norstictic acid is present, as for example in the *Usnea ciliata* complex.

The same method of two-dimensional chromatography was used to check the identity of depsidones in a chemically mixed specimen of the two depsidone-containing races of *Usnea aurantiaco-atra* from the Falkland Islands (*R. I. L. Smith* 2572, AAS). It was also used to establish the identity of salazinic acid and protocetraric acid in Race 2 of the same species from Isla de Los Estudos (Staten Island) which lack norstictic acid. With two-dimensional chromatograms it was sometimes found useful to run an additional control plate containing a mixed extract of the test specimen with known substances as an alternative, or in addition to, running one-way controls in each solvent on the same plate.

The distribution of psoromic acid cannot reliably be used as a diagnostic feature since it occurs randomly throughout the subgenus as it tends to do in quite a few taxa of *Usnea* subgenus *Usnea*. Its presence is apparently of a spasmodic nature and it is frequently only known from a handful of collections in a single species with a different chemistry. It is also of interest to note that in two instances, in *Usnea perpusilla* and *U. sphacelata*, psoromic acid occurs in species which otherwise characteristically lack diagnostic medullary substances. A previous report of psoromic acid in antarctic material of, for example, *U. antarctica* (Golubkova & Schapiro, 1970) is incorrect and refers to an unknown substance (see p. 15).

3. *Fatty acids:* A series of fatty acids which may be of diagnostic importance are found primarily in *Usnea trachycarpa*. These are related to lichesterinic acid and are here referred to as the murolic acid complex. Their chemical structure has already been elucidated by previous authors (Bodo & Molho, 1980; Ghogomu & Bodo, 1982) who found that two of the acids isolated corresponded to murolic and muronic acids, previously known from *Lecanora muralis* (Huneck et al., 1979). Ghogomu & Bodo (1982), using material from Îles Kerguelen, identified the remaining four acids as 13-acetoxyprotolichesterinic acid, 13-acetoxylichesterinic acid, isomuronic acid, and neuropogolic acid. The six acids were found to have Rf values ranging from 0·30 to 0·46 in TA.

The murolic acid complex has here been demonstrated in all three chemical races of *Usnea trachycarpa* throughout its range. These were found to correspond to Rf classes 3 to 5 in TA, using norstictic, psoromic, and stictic acids as markers. Improved separation was obtained when plates were run twice over a distance of 11 cm. Additional acetone extracts were also run in solvent system G (Culberson et al., 1981), designed to separate depsidones with low Rf values. This system also gave improved separation of spots lying approximately between norstictic and stictic acids. Traces of additional substances were sometimes found which made it difficult to identify individual fatty acids. This may indicate that the complex also contains traces of other unknown fatty acids.

A series of fatty acids, apparently belonging to the same complex, has also been found in *Usnea patagonica*. Frequently only two to four fatty acids were detected with the remaining acids absent or only present in trace amounts. The number of fatty acids detected in a single specimen on the TLC plate from this species varied according to the solvent system used or the number of times the plate was run. This may be due to variation in the concentration of the extract spotted on each plate, or, since *U. trachycarpa* uniformly resolved into six spots, may indicate that some different acids are involved which do not separate so readily in the solvent systems used. At least one fatty acid found in *U. trachycarpa* belonging to Rf class 5 in TA did not occur in *U. patagonica*.

At least two fatty acids belonging to Rf classes 2–3 in TA occur in *Usnea neuropogonoides* and are present in both chemical races. These appear to be identical to those of lower Rf classes found in *U. patagonica*.

Very rarely traces of similar, unidentified fatty acids occur in other species in the subgenus, for example *Usnea acanthella*, *U. antarctica**, and *U. subantarctica*, but their presence is not constant enough to warrant taxonomic significance.

4. *Accessory substances:* Throughout the subgenus three undetermined substances were found which produced characteristic coloured fluorescence under long-wave UV light (see Table 2) on chromatograms before charring. On developed plates the spots are either colourless or have slight pinkish or yellow-grey colouration. These substances are here referred to as 'UV + unknowns' and appear at random in most species in the subgenus, with or without medullary substances, and are consequently of no taxonomic value. They are probably unstable or locally concentrated as it was often not possible to repeat the original results from the same thallus. In most species UV + unknowns are only present in trace amounts but in *Usnea perpusilla* they often occur in high concentrations.

Table 2 TLC properties of UV + unknown substances in *Usnea* subgenus *Neuropogon*.

	Rf classes			UV fluorescence		colour of spot
Substance	TDA	HEF	TA	before charring	after charring	(±)
A	3	5	3	pale violet	quench or purple	pale pink
B	2	5	2	pale yellow	greenish grey	pale yellow-grey
C	2	3	1	pale violet	quench or purple	pale pink
D	1–2	3	1	white	quench or purple	colourless

The TLC properties of the UV + unknowns A, B, and C are given in Table 2 along with an additional unknown, D, which fluoresces white under long wave UV light and sometimes occurs in trace amounts with unknown C. Substances C and D may, in trace amounts, be mistaken for fumarprotocetraric or protocetraric acids which have similar Rf classes; however, the characteristic fluorescence of the unknown substances should be a distinguishing feature. Rf classes obtained for unknowns A, B, and C agree with those found by Jørgensen (pers. comm.), working on material from Bouvetøy, in *Usnea antarctica* and *U. aurantiaco-atra*.

The occurrence of these unknown substances in antarctic *Neuropogon* specimens has previously been published by Golubkova & Schapiro (1970). One substance was incorrectly identified by them as psoromic acid and probably corresponds to unknown A. These substances have occasionally been detected in *Usnea s. str.*

Distribution

Figs 4–8

The subgenus *Neuropogon* has a bipolar distribution and largely replaces the subgenus *Usnea* in arctic, antarctic, and subantarctic regions. Only one species, *Usnea sphacelata*, is bipolar, with a circumpolar distribution in the northern boreal regions as well as in Antarctica, and with outliers in the subantarctic and North, Central, and South America. One species, *U. acanthella*, is apparently confined to the northern Andes, whilst the remaining species have antarctic or subantarctic-alpine distributions. Further details are to be found under each species. The distributions discussed here are arranged according to various geographical areas as a background to biogeographical considerations and to substantiate, or comment upon, some records to be found in the literature. Areas where difficulties may arise in identification of species, due to variation or overlap of distributions, are also indicated.

1. *Northern Andean chain*

At present three species, *Usnea acanthella, U. durietzii*, and *U. sphacelata*, are known to occur in

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* Identified as murolic and neodihydromurolic acids by Huneck et al. in *J. Hattori bot. lab.* **56**: 461–480 (1984).

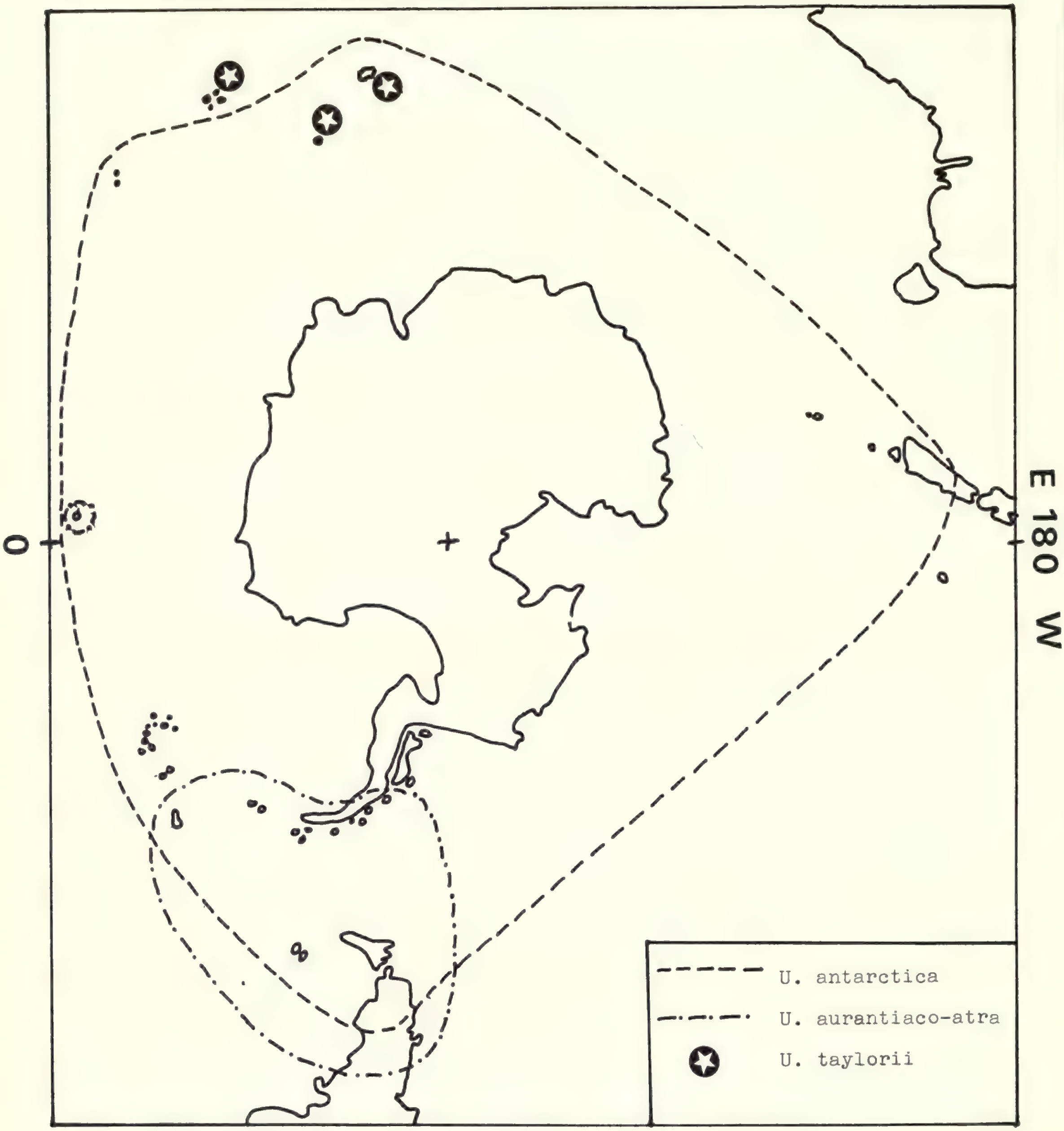

0
E 180 W
U. antarctica
U. aurantiaco-atra
U. taylorii

Fig. 4 Antarctic and subantarctic distribution patterns.

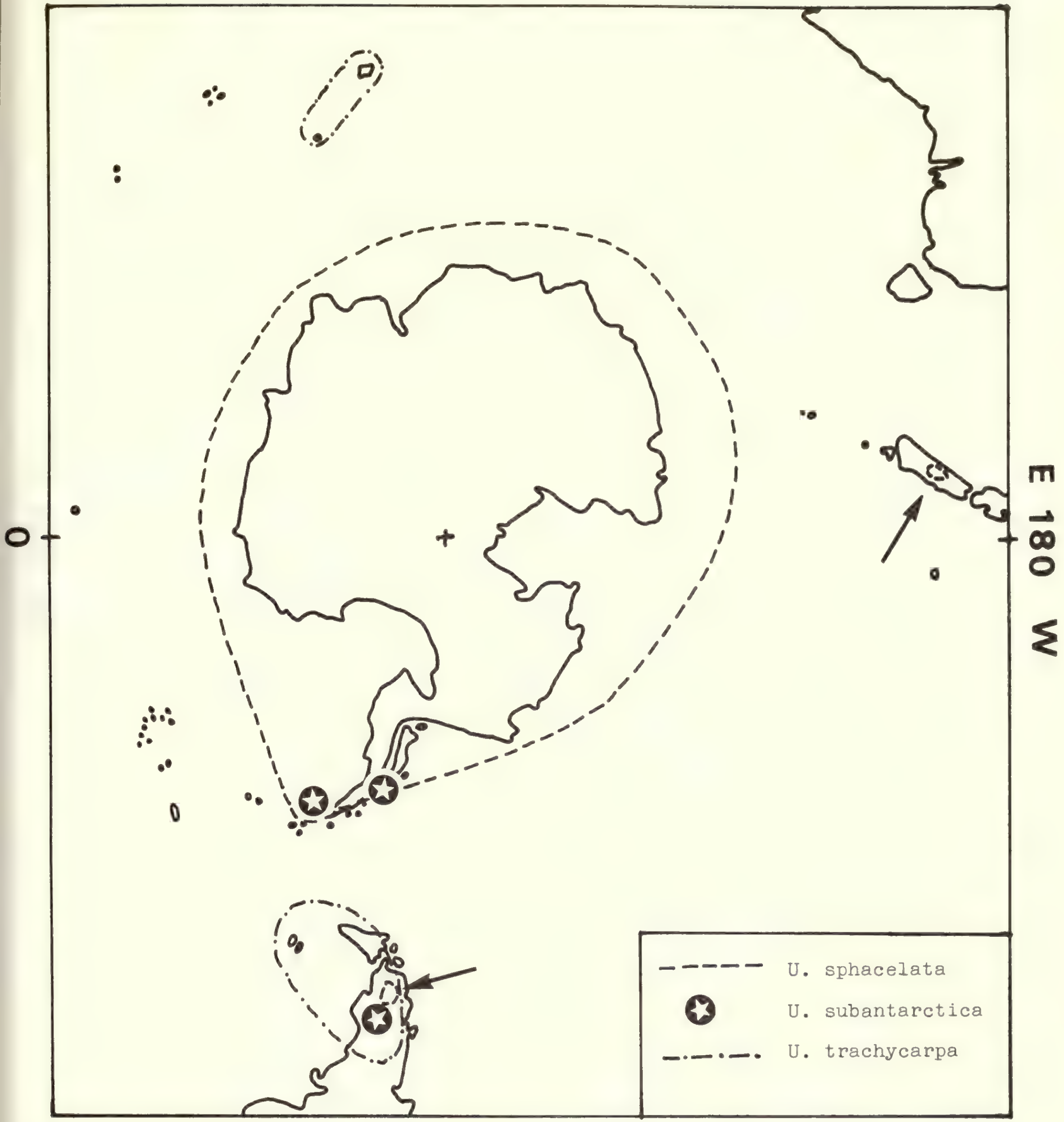

0
E 180 W
U. sphacelata
U. subantarctica
U. trachycarpa

Fig. 5 Antarctic and subantarctic distribution patterns.

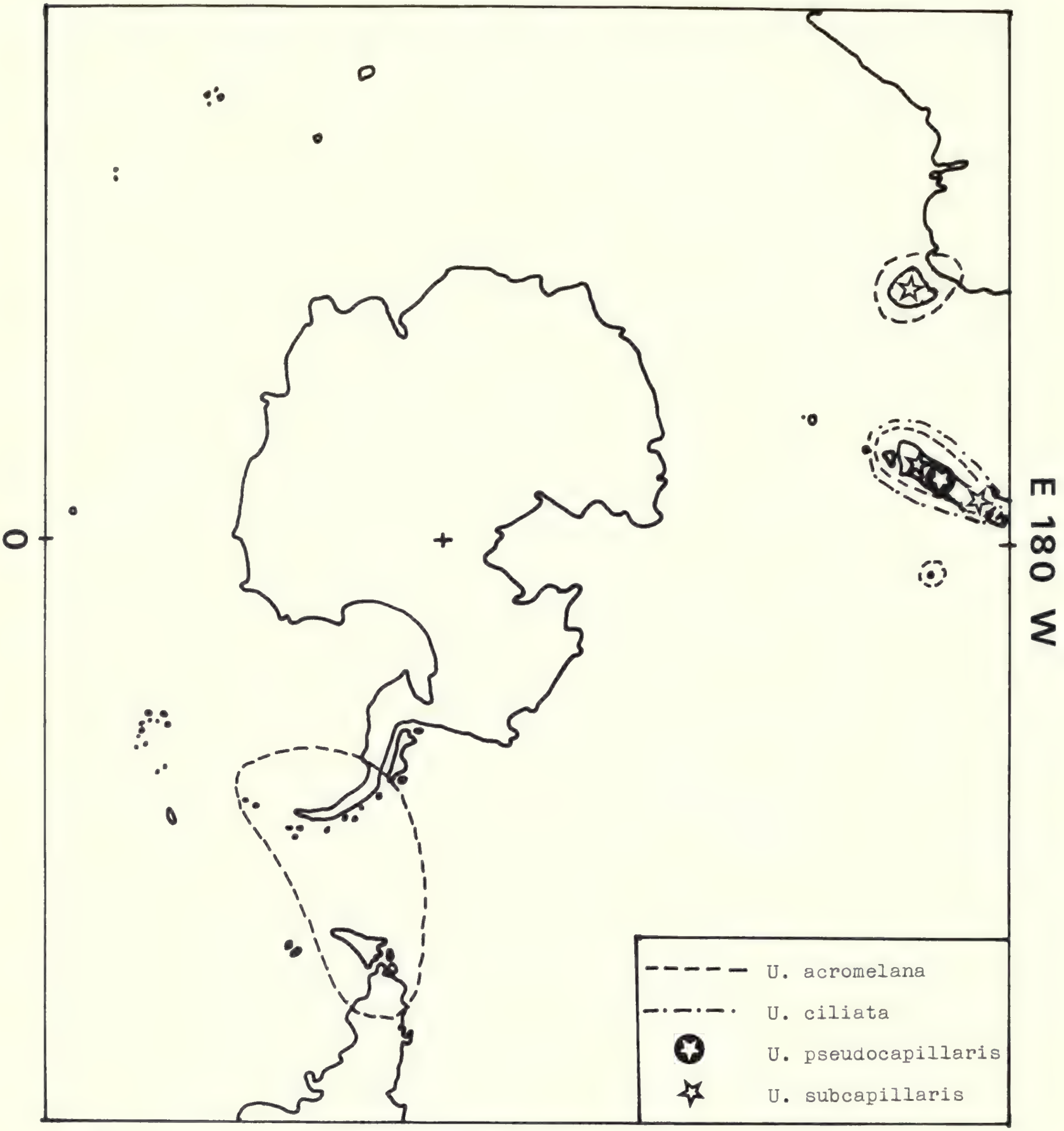

0
E 180 W
U. acromelana
U. ciliata
U. pseudocapillaris
U. subcapillaris

Fig. 6 Antarctic and subantarctic distribution patterns.

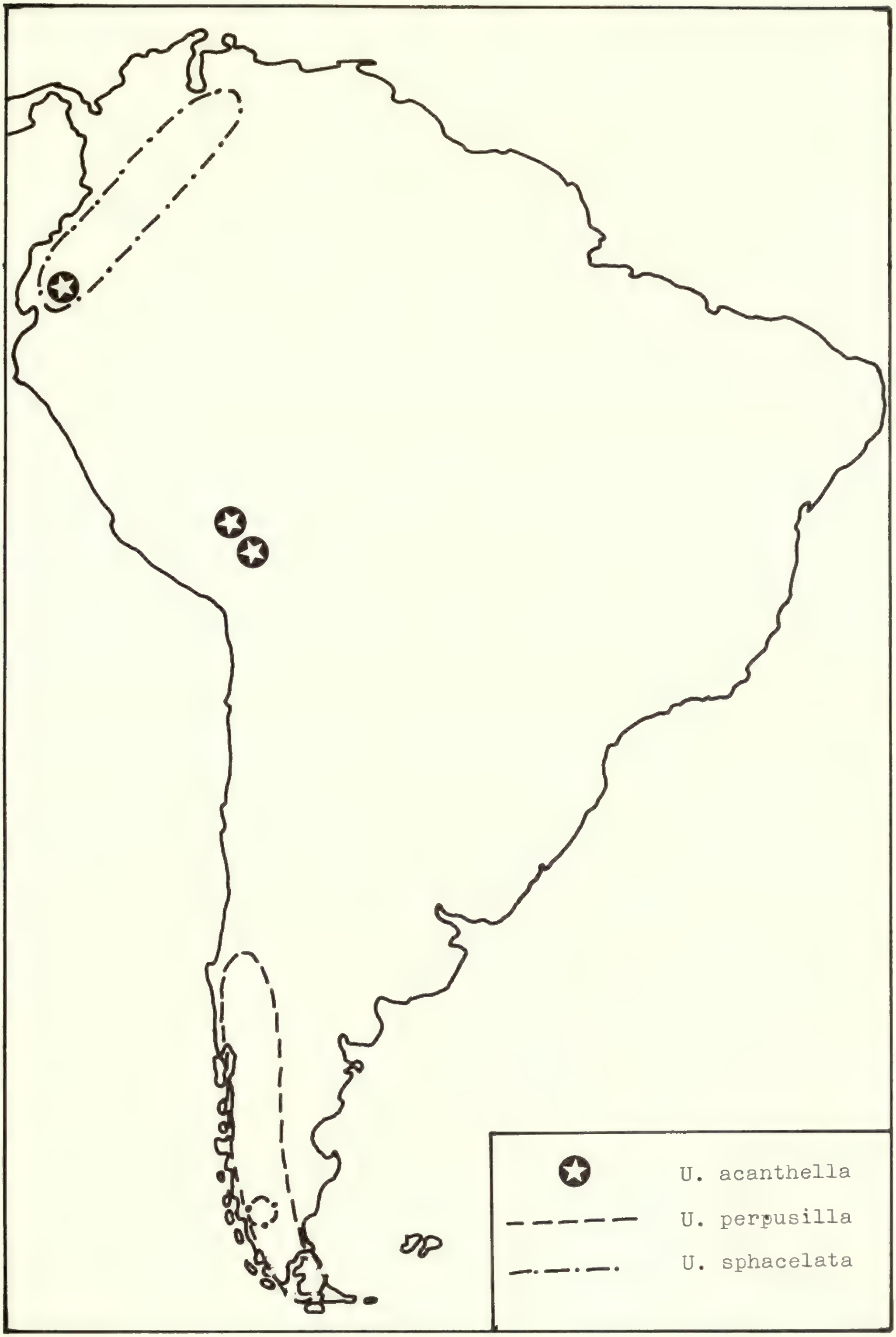

U. acanthella
U. perpusilla
U. sphacelata

Fig. 7 South American distribution patterns.

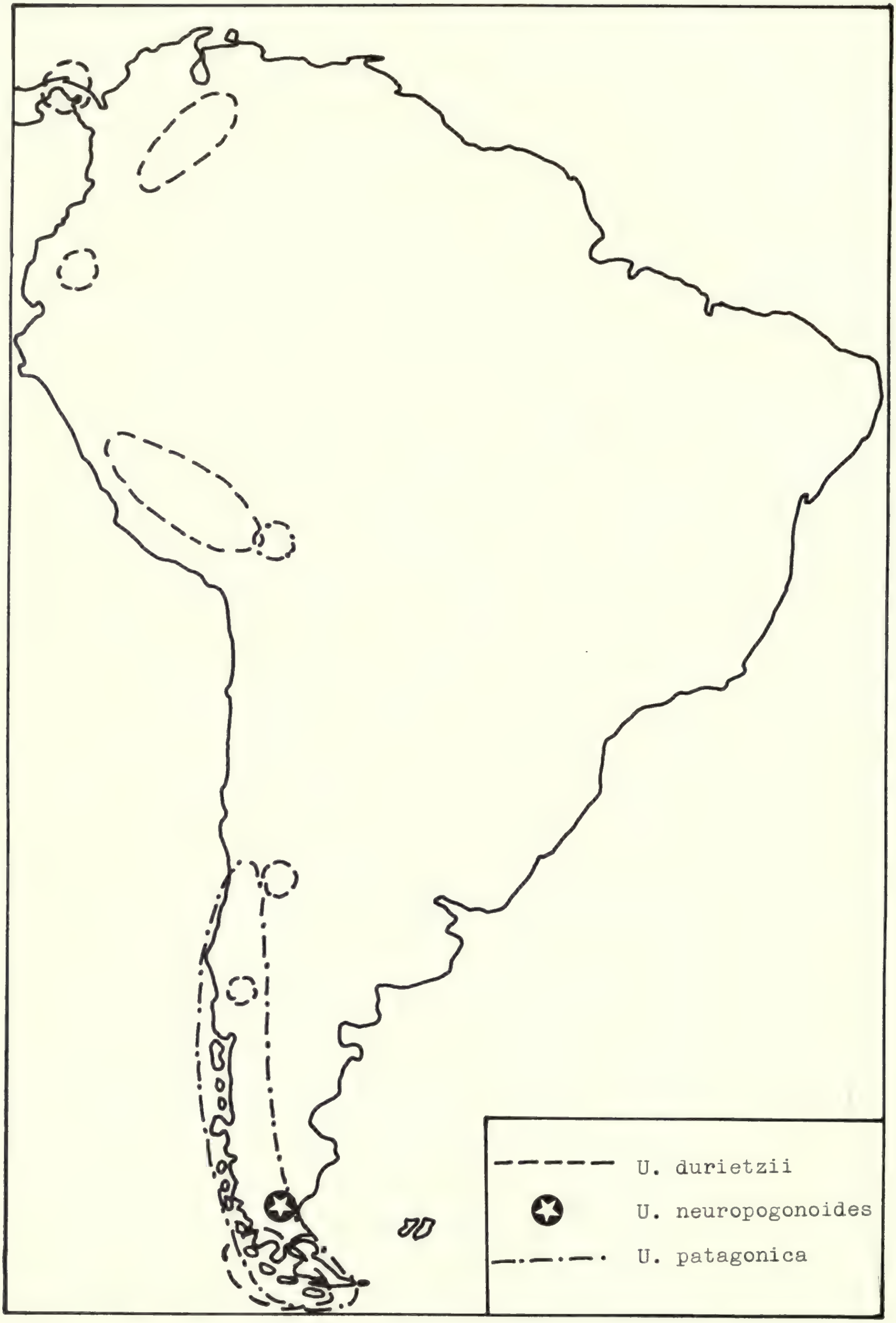

U. durietzii
U. neuropogonoides
U. patagonica

Fig. 8 South American distribution patterns.

this area. The possible occurrence of a fourth species, *U. acromelana*, remains uncertain or doubtful, whilst *U. patagonica* reaches its northern limit in Bolivia. The few collections examined have been referred, where possible, to one of these species, sometimes as atypical forms. Frequently specimens are depauperate, moribund, eroded, or extensively pigmented, and in such instances it is not possible to identify material conclusively.

2. *Subantarctic South America*

This area includes Patagonia, Tierra del Fuego, and the Falkland Islands. The greatest concentration of species occurs in this region with three fertile, one sterile, and six asexually reproducing species known. All three fertile species *Usnea aurantiaco-atra, U. perpusilla*, and *U. trachycarpa* are known as far north as about 40°S. Two other fertile species, *U. ciliata* and *U. taylorii*, have been incorrectly reported from this area, for example by Lamb (1948*a*) and Räsänen (1932), and misidentifications refer to either atypical, smooth forms of *U. aurantiaco-atra*, or weathered forms of *U. perpusilla*. The sterile *U. neuropogonoides* is only known from a small area on the Chilean–Argentinian border. *U. aurantiaco-atra* and *U. trachycarpa* also occur on the Falkland Islands.

The six asexual species found in this area are *Usnea acromelana, U. antarctica, U. durietzii, U. patagonica, U. sphacelata,* and *U. subantarctica*. Some of these species are reaching the limits of their distribution and consequently atypical morphotypes may occur which may lead to misidentification. For example, *U. antarctica* and *U. durietzii* here reach their northern and southern limits respectively. Atypical forms of these two species might be mistaken for *U. patagonica* but fortunately medullary chemistry can be used as an additional guideline since, unlike *U. patagonica*, the two species are usually represented by the depsidone-containing race. Morphological differences between all three species are summarized in Table 3. *U. antarctica* is the only asexual species known from the Falkland Islands and is represented there by a single specimen.

Table 3 Differences between *U. durietzii, U. patagonica,* and *U. antarctica*.

	U. durietzii	*U. patagonica*	*U. antarctica*
Habit/branching	irregular to tufted with short laterals	regular with extended laterals	regular with extended laterals
Pigmentation	apices, base, pseudoisidia	apices, base, pseudoisidia, ± cortex	apices, ± soralia, ± cortex
Medulla	very lax	± lax or sublax	compact
Papillae	rare	± common	common
Soralia	often becoming ± confluent	remaining ± delimited, ulcerose	delimited with crateriform margin
Pseudoisidia	large, *c.* 100 μm	Small, *c.* 50 μm	± absent
Chemistry	norstictic/salazinic acids	deficient/fatty acids	± fumarprotocetraric acid

3. *Australasia*

(a) *Australia:* Two species *Usnea acromelana* and *U. subcapillaris* or possibly three (*U. ciliata*) occur in Australia. The subgenus is uncommon in Tasmania and is extremely rare at very high altitudes in the mountains of Victoria (see below). The majority of specimens examined so far from the mainland are referable to either *Usnea torulosa* or *U. inermis* of the subgenus *Usnea*. Rogers (1981) reported five species (unlisted) from Australia based on catalogues produced by Wetmore (1963) and Weber & Wetmore (1972). These were *U. acromelana, U. antarctica, U. ciliata, U. aurantiaco-atra* (as *U. melaxantha*), and *U. sphacelata*. The epithet *'melaxanthus'* has frequently been misapplied to sorediate material resulting from Nylander's (1855) misconception of the species. Examples include Darbishire (1912), Crombie (1879*b*), and Wilson (1888, 1890, 1893) and again specimens are referable to *Usnea* subgenus *Usnea* or rarely, when in Tasmania, to *U. acromelana*. The record of *U. sphacelata* from Tasmania (Lawrence, 1834) may also refer to *U. acromelana*. *U. antarctica* does not occur in Australia (cf. Filson, 1982).

(i) *Victoria:* Weber & Wetmore (1972) reiterated reports by Wilson (1888, 1890) based on material from Mt. Macedon (37°27′S: 144°34′E) and Mt. Hotham (36°58′S: 147°11′E). Unfortunately Wilson's main herbarium was lost in transit (Filson, 1976). Some duplicate material of Mt. Macedon collections has been traced (NSW!) and specimens belong to the barbatic acid race of *U. torulosa*. To date the only collections of *Usnea acromelana* examined are from the Bogong High Plains (36°45′S: 147°21′E) (MEL 18755!, MEL 1018193!).

(ii) *Tasmania: Usnea acromelana* and *U. subcapillaris* are known from several alpine localities in Tasmania and were previously reported by Lamb (1939*a*) and Bratt & Cashin (1976) respectively. Some specimens of *U. acromelana* examined have close affinities with *U. pseudocapillaris* but are somewhat coarser and are retained in the former species for the present, since a wider range of variation is found than amongst New Zealand populations of *U. pseudocapillaris*. *U. ciliata* may also occur in Tasmania, but unfortunately, I have not seen any definitive, fertile, material. The few examples seen are damaged and lack apothecia and soralia (for example MEL 1029344! and CHR 342744!), and could be either *U. acromelana* or *U. ciliata*. Dodge (1948) cited a specimen, possibly of *U. ciliata*, in herb. Stirton (GLAM) from Mt. Wellington, but this has not been traced. *U. antarctica* was reported from Tasmania by Du Rietz (1929). This was a misidentification of *U. acromelana*, a species which he does not include in his taxonomic treatment (Du Rietz, 1926) since he referred all northern hemisphere material to *U. sulphurea* and all southern hemisphere to *U. antarctica* (Du Rietz, 1929). Wilson's (1893) report of *U. melaxantha* from Table Mountain was based on Robert Brown's collections which mainly consist of *U. acromelana*.

(b) *New Zealand and subantarctic islands*

Five species have recently been recorded from the South Island of New Zealand (Galloway, 1985): *Usnea acromelana*, *U. antarctica*, *U. ciliata*, *U. sphacelata*, and *U. subcapillaris*; a further species, *U. pseudocapillaris*, is described here. Previous reports of *U. aurantiaco-atra* and *U. trachycarpa* (Mark & Bliss, 1970; Martin & Child, 1972) are erroneous and probably refer to *U. ciliata*. The subgenus is commonly represented in alpine areas east of the Main Divide, particularly in central Otago but is rare elsewhere, with *U. antarctica* and *U. sphacelata* confined to a few exposed, predominately high altitude localities. *U. acromelana* and *U. ciliata* are both known from Stewart Island although the subgenus is rare there and is confined to Mt. Anglem (CHR 343356! and CHR 342749! respectively).

The subgenus is very rare in the North Island and, apart from a few recent collections, records are often based on historical data. *U. acromelana, U. ciliata,* and *U. subcapillaris* are all known to occur. One collection from Mt. Ruahine (*Colenso* 1164, WELT!), previously determined as *U. ciliata*, is *Alectoria nigricans*, although another specimen (*Colenso* C1776, BM!, WELT!) from the same locality 'prope Napier' (Müller, 1896) is *U. acromelana*. Both *U. acromelana* and *U. ciliata* are known from Tongariro National Park and the subgenus has recently been refound by Bartlett as far north as Gisbourne, from Mt. Hikurangi in the Raukumara Range (*Bartlett* 25965, BM!) and from the Kaweka Range in Hawkes Bay (*Bartlett* 25961, BM! 25962, BM!), thus verifying the record in Martin & Child (1972).

Only one collection is known from Chatham Island, that collected by Travers (BM!), which is an unusual, decumbent form of *Usnea acromelana*, growing at a much lower altitude than elsewhere in New Zealand. The subgenus does not occur on the Auckland Islands or on Campbell Island, where it is probably replaced by *U. xanthopoga*. *U. antarctica* is the only species examined from Macquarie Island where it is confined to a few localities at the north of the island. Sometimes specimens are somewhat subdecumbent and this has led to misidentifications as that of *U. laxissima* (= *U. sphacelata*) reported by Filson (1981).

4. *Subantarctic islands of the Indian Ocean*

Three species are known, two fertile and one asexual. Of the two fertile species, *Usnea taylorii* and *U. trachycarpa*, the former is only known from Îles Kerguelen and Crozet. *U. antarctica* is known from both island groups as well as from Marion Island in the Prince Edward Island group, thus completing the subantarctic circumpolar distribution of this species eastwards from Bouvetøy. Many sorediate taxa have been described from these islands and all are here regarded as synonymous with *U. antarctica*; the species is represented by a range of rather robust, depsidone-containing variants in this area. Specimens of *U. aurantiaco-atra*, said to have been collected from Îles Kerguelen by Hooker (M!) are unique, and presumably originated from Cabo de Hornos (Patagonia) having been subsequently mislabelled.

5. *Antarctica*

For the purposes of this study Antarctica is here divided into two areas based on geological, climatic, and ecological considerations. The Antarctic peninsula and the antarctic continent as far west as the Ross Ice Shelf are included with the subantarctic islands of the South Orkneys, South Shetlands, South Sandwich islands, and South Georgia and Bouvetøy, and is considered separately from eastern Antarctica, which lies from Dronning Maud Land eastwards to Victoria Land. These approximately correspond to maritime and continental antarctic zones as defined by ecologists, for example Lindsay (1977*a*), although the maritime antarctic usually only includes the west coast of the Antarctic peninsula as far south as Marguerite Bay (Holdgate, 1970). (See 'Phytosociology', p. 28.)

(i) *Antarctic peninsula and islands:* The three most common asexual species are *Usnea antarctica, U. sphacelata,* and *U. subantarctica. U. antarctica* replaces *U. sphacelata* and *U. subantarctica* in the island groups and is often the only species of the subgenus to be found in some localities, for example, the South Sandwich Islands. *U. acromelana* is also found in this area, but is rare or overlooked, and is confined to the northern part of the peninsula and some of the islands. Occasionally all four species may be found in a given locality and may exhibit a bewildering range of variation, besides, with the exception of *U. sphacelata*, sometimes producing apothecia.

Usnea aurantiaco-atra is found on the west side of the Antarctic peninsula, the South Orkneys, the South Shetlands, and on South Georgia. *U. antarctica* and *U. aurantiaco-atra* both occur on Bouvetøy but are rare (Holdgate et al, 1968). The occurrence of *U. trachycarpa* is doubtful, based on a single sterile specimen (*R. I. L. Smith* 3453, AAS!) from the Antarctic peninsula; if supported by further fertile records this would represent a significant extension of its subantarctic distribution.

(ii) *Eastern Antarctica:* Only two species, *Usnea antarctica* and *U. sphacelata*, have been identified from material from eastern Antarctica. Both species are circumpolar, although *U. sphacelata* is the commoner, usually occupying more exposed habitats (pp. 26–27). Where both species do rarely occur together one of them is often depauperate, abnormal, or even somewhat intermediate, and particular thalli may be difficult to identify. Unusual, weathered forms of *U. sphacelata* with a less lax medulla have led some authors (Dalenius & Wilson, 1958; Filson, 1974, 1975; Golubkova & Schapiro, 1970) to confuse this species with *U. acromelana*, a species that is confined to subantarctic regions and only extends its range as far south as the tip of the Antarctic peninsula. The occurrence of unusual forms has also resulted in the description of a spectrum of microspecies which are here reduced to synonymy. Further specimens need to be examined before antarctic distributions can be assessed in detail. A report of *U. aurantiaco-atra* from Dronning Maud Land (Dalenius & Wilson, 1958) is a misidentification of *U. sphacelata* (UPS!). Further problems encountered in this area are discussed under 'Biogeography' (p. 33).

6. *South Africa*
Two collections comprising saxicolous *Usnea* species collected at 1830 m from Cedarberg (*Schelpe* 1961 BOL!, 1966 p.p. BOL!) have been examined and have proved to be very interesting. *Schelpe* 1966 is a mixed gathering of an *Alectoria* species with an unknown, possibly undescribed, *Usnea* species. Thalli have scattered, pigmented, true isidia that are reminiscent of the type found in *Usnea inermis* and, like that species, contain psoromic acid. Part of the second collection (*Schelpe* 1961) was examined by Lamb (1948*a*) and identified as possibly *Neuropogon acromelanus* (CANL 16944!) and *Neuropogon* sp. (CANL 17284!).

Material identified by Lamb as *Neuropogon acromelanus* and part of the original collection (*Schelpe* 1961!) very closely conforms to *Usnea patagonica* and is tentatively referred to that species; for differences between the two see p. 84. Other thalli in this collection and the specimen referred to *Neuropogon* sp. by Lamb do not resemble *Usnea patagonica* quite so closely and remain unidentified. Further material is required, along with detailed study of South African montane species of *Usnea*, including types, before the taxonomic position of the Cedarberg specimens can be finally resolved. Taxa related to *Usnea pulvinata* aggregate, for example *U. capensis*, may also have to be considered.

Since some specimens are tentatively included in *Usnea patagonica* it is remotely possible that the subgenus *Neuropogon s. lat.* is extremely rare at high altitudes in South Africa. Another species with a similar pattern of distribution is *Pseudocyphellaria gilva* which was described from South Africa and is also known from South America. According to Schelpe (pers. comm.) the Cedarberg locality is one of the coldest in the south-west Cape Mountains and is the richest locality for Umbilicariaceae in southern Africa, and consequently is the most likely refugia for any *Neuropogon* species.

Ecology

There has only been a brief opportunity for a first-hand study of the ecological requirements of *Neuropogon* species during the preparation of this account. Consequently much of the information presented here has been drawn from available literature and discussion with lichenologists who have made detailed field observations. As a result many gaps still exist, in particular for South America, and for species which have a restricted distribution or are only known from a few collections.

One of the earliest ecological observations was made by Dumont d'Urville (1826) in his *Flore des Malouines* who noted that (translation) '*Usnea melaxantha (U. aurantiaco-atra)* grew by preference on bare rocks exposed to the south-west winds, forming an unusual type of sward on smooth rock faces. These rocks were always arranged in fairly regular strata inclined at an angle of 40 to 50 degrees and running from east to west'.

This observation reflects the general ecological requirements of the subgenus. These are a more or less acidic, saxicolous substrate and an exposed, predominately arctic-alpine environment which is unfavourable to, and usually excludes, the subgenus *Usnea*. Species are able to flourish in harsh microclimates where temperature variation, radiation, and drought from freezing or high winds, are all major controlling factors. Such conditions are often termed ecological cold-deserts (Lindsay, 1977*a*), since water availability is often the most important factor, and are not necessarily confined to polar regions. Consequently a remarkable altitudinal amplitude is exhibited by the subgenus, ranging from sea-level upwards in polar regions, to *c.* 5000 m in the Andes of tropical America.

In areas where the climate is warmer and the rainfall higher, the subgenus is rapidly replaced by the subgenus *Usnea*. Here *Neuropogon* is confined to exposed, drier, upland areas, as for example, on Macquarie Island and the New Zealand shelf islands. *Neuropogon* species are rarely able to compete with the subgenus *Usnea*; an exception is *Usnea acromelana* which occupies similar habitats to *U. torulosa*.

Species of *Neuropogon* are adapted ecologically, morphologically and physiologically (Ahmadjian, 1970) to these cold-desert conditions which impose stresses that are rarely encountered elsewhere (Lindsay, 1977*a*). The presence of a thick cortex is probably an adaptation against water loss and, conversely, water uptake (Ahmadjian, 1970), although the latter can still occur via the soralia. In addition much mechanical strength, as found in the tough axial strand, is required to withstand wind-blast.

It has often been observed that pigmented lichens are more frequent in Antarctica, and Lindsay (1977*a*) noted that thalli of *Usnea sphacelata* are more heavily pigmented in continental than in maritime Antarctica. This pigmentation may provide protection for the underlying algal cells against UV radiation (Ahmadjian, 1970), but more importantly absorbs heat which may assist in melting snow (Lindsay, 1977*a*) and increase carbon assimilation (Kershaw, 1983).

Neuropogon species have to withstand a great range of temperatures (Lindsay, 1977*a*) and their metabolism shows a remarkably effective physiological adaptation to low temperatures, particularly when dry, and hence may be described as facultatively or obligatively psychrophilic (Lamb, 1970). Field and laboratory measurements of respiration and photosynthetic rates (Ahmadjian, 1970) have shown that thalli of *Usnea sphacelata* are able to maintain a positive metabolic balance of temperatures as low as −18·5°C, whilst a negative balance occurs above +20°C. Consequently an extended period of high temperatures would be damaging.

Distribution of the subgenus is controlled by climatic, edaphic, and biotic factors (i.e. bird rookeries) (Lamb, 1970). Consequently there are few habitats in the polar regions where species of *Neuropogon* do not occur. Despite being able to withstand severe physiological drought, it is evident that some moisture is essential, either as mist or melt-water, although this requirement varies considerably according to the species. For example, in New Zealand species of the *Usnea ciliata* complex are absent from areas where there is prolonged snow cover, including the bases of exposed tors on mountain plateaux and in fellfields (Mark & Bliss, 1970). Such intolerance towards prolonged snow cover is similar to that exhibited by *Parmelia olivacea* in Scandinavia (Ahti, 1966).

This is in contrast to some other macrolichens, for example *Umbilicaria cylindrica* (Mark & Bliss, 1970) and *Cladonia bellidiflora* (Lynge, 1937), which appear to require prolonged winter snow protection against wind-blast. Similarly in New Zealand, the *Usnea ciliata* complex is rarely found in the nival zone above the permanent snow-line, or in areas of permanent glaciation. In contrast *U. sphacelata*, a species that has its main distribution in the polar regions, is best adapted to withstand much harsher climatic conditions and, for this reason, mainly occurs in New Zealand (and Patagonia), in very exposed, snow-free, alpine areas and nunataks at higher altitudes.

The distribution of *Neuropogon* species on the Antarctic continent, excluding the Antarctic peninsula, appears to be very local, thus reflecting the availability of suitable habitats which are limited to ice-free coastal areas and exposed nunataks (Ahmadjian, 1970). For example, the subgenus was not found on Mawson Rock, Mac. Robertson Land (Seppelt & Ashton, 1978) although species of *Alectoria, Umbilicaria,* and *Xanthoria* occurred, but has been recorded from many other localities to the west (Filson, 1966, 1975). There are also many localities where, as a result of under-collection, the subgenus has not been previously reported, for example at Hallett Station, Victoria Land (Rudolph, 1963, 1967).

On the antarctic continent inland areas often receive more sunshine than coastal areas (Lamb, 1970) and consequently melt-water streams sometimes flow from inland nunataks to coastal outcrops allowing subsequent colonisation (Filson, 1982). The subgenus appears to have a southern distributional limit, since it is often absent from localities that might be considered favourable that support *Umbilicaria* species (Lindsay & Brook, 1971), although duration of snow-cover may again be a critical factor. Microlichens extend further south than macrolichens (Lamb, 1970; Siple, 1938). This may be due to the narrowing of the boundary layer of warmer air through which fruticose lichens extend (Kershaw, 1983), coupled with an increase in the effect of ice-blast, the relative harshness of which increases with decrease in temperature (Lindsay, 1977*a*). This is enhanced by the constant katabatic winds (Lamb, 1970; Greene & Longton, 1970) which, combined with the freeze-thaw action may modify thallus morphology (Filson, 1982).

Edaphic factors are important since most species are obligate saxicoles, although a few may rarely secondarily occupy more diverse substrates. For example, *Usnea antarctica* may occasionally grow on bryophytes, discarded timber, eroded peat, or soil (Lindsay, 1973, 1978; Smith & Corner, 1973), although the range of habitats it is able to colonise decreases towards its southern limit of distribution. Similarly, the South American species, *U. acanthella* and *U. neuropogonoides*, may become detached or fragmented and assume a terricolous habitat.

The subgenus almost always occurs on acidic rocks and is regarded as calciphobous; it is only able to colonise stable ground (Smith, 1973). For example, in New Zealand, the species of the *Usnea ciliata* complex are virtually confined to chlorite schists and, to a lesser extent, greywacke or, rarely, rocks of volcanic origin. In contrast, in the subantarctic regions, *U. antarctica* is often found on volcanic rocks and lavas, for example on Macquarie Island (Huntley, 1971) and on Marion and Prince Edward Islands (Lindsay, 1977*b*), although the species is unable to grow in the vicinity of active fumaroles that occur, for example, on the South Sandwich Islands (Longton & Holdgate, 1979). Similarly, in Patagonia, *Neuropogon* species are found on a wide range of substrates from lavas to basaltic rocks and sandstones.

Observations in continental Antarctica (Siple, 1938) have shown that whilst *Usnea antarctica* and *U. sphacelata* both occurred on granitic and metamorphic sediments, such as schists and sandstones, *U. antarctica* was more widely distributed on the former. This species is also calciphobous since studies of schist-marble boundaries (Gimingham & Smith, 1970; Smith, 1973) show an abrupt demarkation at the interface. Similarly in the arctic, Lynge (1941) observed that *U. sphacelata* was common on basaltic or siliceous deposits and did not occur on purely calcareous rocks, although recent collections indicate that this species may rarely occur on slightly calcareous rocks (E. Hansen, pers. comm.) and sandstones.

It may be possible that the hardness of the rock in addition to its composition may also influence colonisation. For example, on the Kar Plateau, South Victoria Land, *Usnea antarctica* was found to occur on dolerite boulders covered with a wind-blown deposit of sandstone grit (Schofield, 1972), thus providing a more suitable substrate. Similarly, in New Zealand, strongly foliated schists are easily colonised (Mark & Bliss, 1970).

In addition to substrate composition aspect is also important in relation to microclimate. Despite being able to tolerate very exposed conditions, it is often noticeable that some degree of shelter is necessary against wind or, in maritime environments, against salt-spray. Field observations in New Zealand have shown that the growth of species of the *Usnea ciliata* complex is more luxuriant on the underhangs of sheltered vertical sides of tors and exposed ridges than on horizontal faces. *U. subcapillaris*, and presumably *U. pseudocapillaris*, tend to favour more sheltered habitats and crevices.

Similarly in Antarctica, *Usnea antarctica* occurs in more sheltered habitats than *U. sphacelata* and consequently the species is usually found at lower altitudes, often growing more luxuriantly some distance inland than at sea-level (Lamb, 1964) due to mist-formation caused by coastal temperature inversions (Lindsay, 1977*a*). Where both species occur together in continental Antarctica, *U. antarctica* is generally rare (Dodge, 1962; Øvstedal, 1978) and poorly developed, as it is just surviving at the southern limit of its distribution. Thalli are often small, atypical, and as such may be difficult to identify conclusively. Consequently communities dominated by *U. antarctica*, that are frequent in the subantarctic regions and on the Antarctic peninsula, are rare in continental Antarctica, being restricted to sheltered habitats (Longton, 1973). In contrast, *U. antarctica* cannot tolerate excessive moisture. For example on the South Shetland Islands, this species is found in a community with bryophytes and *Umbilicaria antarctica* where melt-water collects, but is only prominent on dry surfaces and south-facing aspects (Lindsay, 1971*a*).

Within the subgenus species exhibit varying ecological requirements and tolerances, with asexual species often having wider distributions and occupying a wider range of habitats than their fertile counterparts. The absence of any sexually reproducing species from continental Antarctica may primarily be controlled by environmental conditions rather than distributional factors. Hawksworth (1973), in discussing ecological differences between primary and secondary species, observed that greater soralia production occurs in humid situations and that sorediate species are more able to utilise atmospheric moisture.

For example, *Usnea antarctica* has much broader requirements than *U. aurantiaco-atra*, being able to colonise more varied habitats and occupy a wider range of altitudes (Lamb, 1964;

Lindsay, 1971*a*). *U. aurantiaco-atra* is regarded as a montane, maritime species (Lindsay, 1971*a*; 1977*a*) which tends to favour slightly more sheltered aspects (Smith & Corner, 1973) and is less tolerant of strong winds (Smith, 1973). This species is unable to produce mature spores towards the southern limit of its distribution (Lindsay, 1971*a*). *U. antarctica*, in contrast to *U. aurantiaco-atra*, is slightly tolerant of nutrient-enriched melt-water (Lindsay, 1969, 1971*a*). This species is usually regarded as indifferent rather than nitrophilous (Lamb, 1964, 1970), since it may sometimes grow in nitrogenous habitats around bird rookeries with, for example *Caloplaca regalis, Xanthoria elegans*, and *Lecanora aspidophora* (Lindsay, 1971*a*). Both species of *Usnea* are regarded as halophobous (Lindsay, 1971*a*), being replaced in coastal communities by *Ramalina terebrata* (Follmann, 1965*b*), although *U. antarctica* may be able to tolerate some salt spray.

From general observations on the distribution and ecology of *Usnea antarctica* and *U. sphacelata* throughout their respective ranges, it is apparent that the latter is characteristically a species of exposed habitats, usually not in close proximity to the sea, and is consequently the more common species is continental Antarctica. Consequently in the arctic, this species is only found where the climate is sufficiently continental (Bliss, 1981; Greene & Longton, 1970; K. Hansen, 1962; Lindsay, 1977*a*, 1978). The somewhat restricted distribution in the arctic may therefore be due to climatic as well as biogeographical factors, although its absence from large continental areas may be due to under-collecting rather than ecological reasons (E. Hansen, 1982).

Lamb (1964), from studies in the Antarctic peninsula, indicated that although the distributions of the two species overlap, *U. sphacelata* is often found at higher altitudes than *U. antarctica* and has a somewhat southerly and easterly distribution in that area. On the Antarctic peninsula *U. sphacelata* is often replaced by *U. subantarctica* at low altitudes, a species that appears to have ecological requirements that are intermediate between the other two species.

In the subantarctic regions species occur that have different ecological requirements from the antarctic–arctic species. The requirements of the *Usnea ciliata* complex have already been discussed and these species from an alpine–southern temperate element which, in Patagonia, is represented by *U. perpusilla* and *U. acromelana*. In addition in this area a specialised group of species is prominent which may be referred to as a transitional arid-montane element. This comprises *U. durietzii, U. neuropogonoides, U. patagonica*, and *U. trachycarpa*, which are characteristic of areas of low rainfall between the main high Andean Cordillera and the Patagonian plains, although often extending into both areas. Such species occupy a variety of habitats and, although often occurring with arctic-alpine or alpine southern–temperate species, are primarily adapted to open, exposed, dry but misty, rather than necessarily polar–alpine, habitats.

Phytosociology

Antarctica and the surrounding subantarctic regions have been divided into various ecological zones, primarily based on phanerogamic communities, by numerous workers (see Holdgate, 1970), and those defined by Longton (1966) have been most widely accepted. Three main zones are recognised: the southern cold-temperate, the subantarctic, and the antarctic, based on the position of the subtropical and Antarctic Convergences (Holdgate, 1970; Skottsberg, 1960).

The subantarctic regions have been variously defined (Bliss, 1979; Godley, 1960; Greene, 1964*a*; Skottsberg, 1960; van Zinderen Bakker, 1971; Wace, 1960) and various islands are included that lie in the vicinity of the Antarctic Convergence, either side of which marked climatic, and hence vegetational differences occur. For example, although South Georgia and Isla de Los Estados (Staten Island) lie on approximately the same latitude, the snow-line on the former is lower than the tree-line on the latter (Deacon, 1960). Consequently South Georgia has been included in the subantarctic zone for floristic and climatic affinities (Greene, 1964*a*, 1964*b*; Lindsay, 1975), although possessing affinities with both the antarctic and subantarctic regions (Bliss, 1979).

Similarly various classifications of arctic vegetation have been proposed, which have been summarised by Bliss (1981). Bliss (1979, 1981) has also recently described a new classification for the vegetation of polar and alpine regions based on integrated ecological information. Broadly, various biomes (arctic, subarctic; alpine, subalpine; antarctic, subantarctic) were defined and each divided into low and high zones according to altitude or latitude. Within this regime each high zone may be further subdivided into desert and semi-desert units, thus reflecting the concept of ecological cold-deserts of Lindsay (1977*a*).

This classification is much more flexible than earlier proposals since it is not based primarily on strict geographical or climatic boundaries. Subdivisions of each biome are based on the distribution of key genera which, in the polar desert subdivisions includes bryophytes and lichens. Consequently a particular island or region may support different vegetation zones and be placed in the relevant divisions, thus supporting evidence that gradients exist between zones (Longton, 1967).

The divisions maritime (or oceanic) and continental antarctic (Holdgate, 1970) are retained here for convenience, since they reflect the distribution and ecology of particular *Neuropogon* species, although both are included in the polar desert subdivisions of the high antarctic biome by Bliss (1979). The maritime antarctic includes Bouvetøy, the South Sandwich Islands, the South Orkneys, South Shetlands, the Palmer Archipelago, and the western coast of the Antarctic peninsula as far south as Marguerite Bay. Continental Antarctica has been further subdivided into three zones (Holdgate, 1970; Schofield, 1972), but these are not discussed here. As a result of climatic differences, lichen communities in the maritime antarctic are more diverse, having some affinities with those of the boreal-arctic zones, than those found in continental Antarctica which are local, less diverse, and show affinities with the high arctic (Lindsay, 1978).

Antarctic

A range of lichen and bryophyte phytosociological communities have been described from the antarctic and subantarctic regions which reflect the general ecological differences that occur between *Neuropogon* species. In contrast, little ecological work has been undertaken in continental Antarctica and frequently communities described do not contain *Neuropogon* species. The most detailed research has been undertaken in the maritime antarctic (Allison & Smith, 1973; Gimingham & Smith, 1970; Lindsay, 1969, 1971*a*; Longton & Holdgate, 1979; Redon, 1969, 1973; Smith, 1973; Smith & Corner, 1973) of which three groups are relevant: those in which *Neuropogon* species either form a major component, or are less important, or are absent.

Fruticose and foliose lichens predominate (Lindsay, 1977*a*) and three major community types dominated by *Neuropogon* may be recognised. The *Usnea antarctica* sociation is characteristic of windswept, gravel-covered cols, and windgaps; whilst that of *U. aurantiaco-atra* (as *U. fasciata*) is found on boulder-fields; and that of *U. sphacelata* (as *U. sulphurea*) is more characteristic of the east coast of the Antarctic peninsula and continental Antarctica. The first two community-types only are discussed in more detail below. Habitats on the west coast of the peninsula become drier with increasing latitude (Longton, 1967) and consequently vegetation is much sparser and communities less complex, when, for example, those of the Argentine Islands are compared with the South Orkneys (Smith & Corner, 1973).

Usnea antarctica is the most widespread *Neuropogon* species in the maritime antarctic, and many communities have been based on this species, for example the alliance *Neuropogonion antarcticum* (Follmann, 1967). *U. antarctica* is the dominant species in the *Andreaea-Usnea* sociation on the South Orkneys (Smith, 1973) and forming the *Usnea antarctica* sociation on the South Shetlands (Smith, 1973, 1984) and South Orkneys (Allison & Smith, 1973), which is rare in continental Antarctica (Longton, 1973). The species is also found in the *Lecideetum sciatraphae* (Follmann, 1967). It is often a primary coloniser (Lindsay, 1978) of boulders in moraines and there is often a succession of *U. antarctica* followed by crustose species, including *Buellia anisomera* and *B. russa* (Lamb, 1970), although the reverse has been observed (Lindsay, 1978). Moss banks may be colonised by a range of lichen species (Smith, 1973) including

Ochrolechia frigida, Cladonia rangiferina, Sphaerophorus globosus, and *U. antarctica*, when the growing tips of the mosses are not covered by snow. *U. antarctica* is the major component of the *Sphaerophoretum teneri* (Redon, 1969) and is occasionally found in more halophobous communities with *Himantormia lugubris* and *Andreaea* species (Allison & Smith, 1973).

In contrast *Usnea aurantiaco-atra* occurs in much more halophobous and nitrophobous communities than *U. antarctica*. For example, on the South Orkneys this species forms a distinct community on raised beaches with *Himantormia lugubris* over a range of a latitude with species of *Andreaea, Rhizocarpon,* and *Lecidea*. *U. aurantiaco-atra* is also found in communities with halophobous species, including *Sphaerophorous* and *Stereocaulon*. Lindsay (1971*a*) has described a series of communities along a gradient away from a slightly nitrophilic habitat dominated by *U. antarctica* that is finally replaced by the *U. aurantiaco-atra–H. lugubris-Andreaea* sociation.

Occasionally communities may contain both *Usnea antarctica* and *U. aurantiaco-atra* (Smith, 1973). *U. antarctica* is characteristic of dry deposits of fine gravel and sandy soil and is often replaced on exposed, windswept ridges by *U. aurantiaco-atra* and *Himantormia lugubris*. However, *U. aurantiaco-atra* is also found in an *Usnea–Umbilicaria–H. lugubris* sociation on dry, exposed rock faces at higher altitudes, which are dominated by *U. antarctica* and species of *Buellia, Lecidea* and *Rhizocarpon*. Similarly, in the *Andreaea–Grimmia–Usnea–Umbilicaria* sociation (Smith & Corner, 1973) *U. antarctica* is the most prominent species on windswept outcrops whilst *U. aurantiaco-atra* is only locally abundant in slightly more sheltered situations.

Subantarctic

The subantarctic islands are all characterised by an extremely cool, oceanic or maritime climate with little annual or diurnal temperature variation (Du Rietz, 1960), high rainfall, constant high humidity, and strong westerly winds (Eaton, 1879; Greene, 1964*a*; Wace, 1960). Lichen communities are not so prominent, being confined to very exposed rocky situations on, for example, Marion Island (Lindsay, 1977*b*) and Macquarie Island (Filson, 1981). Consequently most ecological and floristic work has been concentrated on phanerogamic communities (Greene, 1964*a*, 1964*b*; Hooker, 1879*a*, 1879*b*; Taylor, 1955; Wace, 1960). Two species, *Usnea antarctica* and *U. aurantiaco-atra*, that are characteristic of the maritime antarctic, occur in this region, with the latter being replaced by *U. taylorii* beyond the eastern limit of its distribution in similar habitats (Dodge & Rudolph, 1955). *U. trachycarpa* also occurs on Îles Kerguelen but is characteristic of exposed, dry, windswept, rather than alpine, habitats. Consequently the species of *Neuropogon* occurring in the subantarctic are a mixture of antarctic and cold-temperate elements, bearing strongest affinities with the maritime antarctic.

The lichen flora of South Georgia has affinities with the other subantarctic islands, Tierra del Fuego, the Falkland Islands, and the Scotia Arc. Communities dominated by fruticose and crustose lichens (Lindsay, 1975) were found to be similar to those of the South Orkneys. For example, an *Usnea aurantiaco-atra* (as *U. fasciata*)-crustose lichen community was widespread on moderately exposed, dry, boulders and cliff faces in which *U. aurantiaco-atra* often gave 80% cover with an understorey of mosses, *Lecidea, Lecanora, Pertusaria,* and *Rhizocarpon* species. In contrast at lower altitudes an *U. antarctica*-crustose lichen community, tolerant of slightly nitrogenous melt-water, had less cover of *Neuropogon* and a greater variation of crustose lichen understorey. *U. aurantiaco-atra* also occurs in a markedly nitrophibous community, which has a restricted distribution in very dry situations at high altitudes, in which *Pseudephebe pubescens* and *Alectoria miniuscula* were often co-dominant, forming an understorey which virtually excluded crustose lichens and mosses.

Lichen communities on Marion and Prince Edward Islands have been briefly outlined by Lindsay (1977*b*). Communities on Marion Island were found to be local on exposed ridges and dominated by *Usnea, Alectoria, Himantormia,* and *Umbilicaria* species. *U. antarctica* (as *U. insularis*) was an associated species in a community dominated by *Lecidea* species on moderately exposed boulders and rock-faces. Little revision has been made of the lichen flora of Îles Kerguelen since that made by Crombie (1876*a*, 1877, 1879*a*) of Hooker's work (Hooker &

Taylor, 1844; Hooker, 1847) apart from Dodge's contributions (Dodge, 1948, 1966). Crombie (1879*a*) reported *U. taylorii* from high altitudes on Îles Kerguelen and his other records refer to *U. antarctica* and *U. trachycarpa* which may sometimes occupy the same habitats.

Southern cold temperate

The southern cold-temperate zone has been variously defined (Darlington, 1965; Godley, 1960; Holdgate, 1970; Skottsberg, 1960) and very broadly encompasses regions of southern South America (including the Falkland Islands), New Zealand and the associated shelf islands, and even the south-eastern corner of Australia with Tasmania. In these regions most *Neuropogon* species reach their northern distributional limit and are primarily represented by a group of species that may be termed alpine–southern temperate, rarely with isolated occurrences of antarctic or subantarctic species.

In Australasia this element is well-represented by the *Usnea ciliata* aggregate. Little ecological work has been undertaken in this region apart from studies in Central Otago, New Zealand by Mark & Bliss (1970). Similarly, little is known of the alpine lichen flora of Tasmania, where *Neuropogon* species are rare and confined to relatively few high altitude localities (*c.* 850–1250 m). The dominant alpine phanerogamic vegetation is different from that of New Zealand (Kirkpatrick, 1980) which indicates that climatic and vegetational differences exist at corresponding latitudes which exclude *Neuropogon*.

Recent observations on the Rock and Pillar Range, Otago, have shown that a characteristic community, dominated by *Neuropogon* species, occurs on exposed, isolated rock tors in *Celmisia-Poa* herbfield at the boundary (*c.* 1200 m) of the low and high alpine zones (Mark & Bliss, 1970) or biomes (Bliss, 1981). Such communities were dominated by *Usnea acromelana* and *U. ciliata* with occasional small thalli of *U. subcapillaris*. Associated species included *Alectoria nigricans, Coccocarpia palmicola, Hypogymnia lugubris, Lecanora polytropa* aggr., *Lecidea* spp., *Menegazzia aeneofusca, M. castanea, M. lucens, M. nothofagi, Parmelia petriseda, Pertusaria dactylina, P. superba, Umbilicaria* spp., and *Usnea torulosa*.

At lower altitudes *Usnea ciliata* is much rarer, for example on Mt. Maungatua, Otago (*c.* 880 m) and only *U. acromelana* was found growing with *U. torulosa* on scattered tors in tussock grassland. At even lower altitudes, *c.* 370 m, on an exposed plateau at the foot of the Rock and Pillar Range, only *U. acromelana* was found. This species was only represented by a few deformed thalli on schist boulders in a community dominated by *Parmelia* and *Xanthoparmelia* species, including *P. mougeotina, P. petriseda, P. pseudosorediosa, P. reticulata, P. signifera, P. subrudecta, P. sulcata, X. mexicana,* and *X. tasmanica.* Associated species included *Buellia macularis, Lecanora blanda, Lecidea irrubens, Rhizocarpon geographicum* aggr., and *Siphula coriacea*.

The climate of southern South America is more oceanic than at corresponding latitudes in the northern hemisphere and, in some respects, is more like the montane climate of the equatorial Andes (Troll, 1960). The mountainous Magellanic archipelago provides few habitats that are sufficiently dry (Holdgate, 1960) for *Neuropogon* species. A southerly decrease in the level of the permanent snow-line and a sharp climatic gradient from west to east (Auer, 1960) provides a wide range of habitats and hence communities. The mountainous region of the Argentine–Chile border is subject to almost constant winds and frequent storms (Shipton, 1959) which impose rigorous conditions. There is an abrupt change to the east from *Nothofagus* forest on the slopes of the higher mountains to the grasslands of the lower hills and undulating plateaux (Shipton, 1959) which extend eastwards to form the dry, semi-desert plains (mesetas) of Patagonia (Darlington, 1965).

Ecological studies have previously primarily been directed towards the classiciation of phanerogamic vegetation (Godley, 1960; Holdgate, 1960; H. Weber, 1969). Previous lichenological investigations have mainly been taxonomic, adding to distributional records (Crombie, 1876*b*; Grassi, 1952; Lamb, 1948*a*, 1955; Räsänen, 1932, 1939; Redon, 1972; Santesson, 1942) with little ecological investigation (Lamb, 1959; Mattick, 1951). Lamb (1959) made brief reference to a saxicolous alpine community composed of species of *Neuropogon* associated with

Lecidea species, *Pseudephebe pubescens, Rhizocarpon adarense,* and *Umbilicaria decussata*, which was found to be a mixture of antarctic and subantarctic elements and was similar to those described from central Chile (Follmann, 1965*a*; Redon, 1973) probably based on *U. patagonica* (as *U. acromelana*). Redon (1972, 1974) described various alpine communities from Chile and found them to be similar to those occurring on the Argentinian side of the Cordillera. *U. aurantiaco-atra* was found in a community with *Rhizocarpon geographicum, R. crystalligenum, Umbilicaria cylindrica,* and *U. nylanderiana*.

Altogether ten species of *Neuropogon* are found in southern South America which may be grouped into various floristic elements that form distinct communities or intergrade. *Usnea sphacelata* represents a continental antarctic element that is confined to high alpine areas, particularly those associated with areas of glaciation. *U. antarctica*, *U. aurantiaco-atra*, and *U. subantarctica* represent the northern limit of a maritime antarctic element. Alpine southern-temperate species are represented by *U. acromelana*, which is restricted to glacial valleys and moraines, and the endemic *U. perpusilla* which tends to replace *U. aurantiaco-atra* towards northern Patagonia. Perhaps the most interesting group of species are those which form a transitional arid-montane element, represented by *U. durietzii, U. neuropogonoides, U. patagonica,* and *U. trachycarpa,* which occur within a wide range of altitudes and are capable of extending into the mesetas as well as the lower alpine slopes of the Cordillera.

Consequently many unusual communities occur which contain several of these floristic elements. For example, on the lower mountains of Tierra del Fuego, at *c.* 800 m, collections have been examined consisting of *U. antarctica* and *U. cf. subantarctica*, together with unusually fibrillate forms of *U. aurantiaco-atra*, *U. perpusilla*, and *U. trachycarpa*.

The lichen flora is less diverse on the Falkland Islands since low altitude, maritime communities containing *Usnea antarctica* are absent, possibly due to univestigated ecological factors or extinction due to changes in land-use. Only remnants of a unique lichenicolous heath community (Standring, 1983) now remain which support *Protousnea* species (Krog, 1976), and which is probably closely related to the Magellanic moorlands of Chile. On these islands strong winds, rather than low temperatures, favour the growth of *U. trachycarpa* whilst the maritime antarctic element is represented solely by *U. aurantiaco-atra*.

Tropical-alpine

The climate and the flora of the tropical high mountain zone of Central and South America have been compared to that of the subantarctic (Darlington, 1965; Troll, 1960; Wace, 1960) as for example, seen by a comparison of tussock grassland and the páramos. By contrast, these vegetation types are very different from those of the cold-temperate zone of the northern hemisphere. For example, in Ecuador, at Quito (2850 m) there is great diurnal but little annual temperature range (Troll, 1960) whilst at higher altitudes, close to the permanent snow-line (e.g. Mt. Chimborazo, *c.* 4750 m) there is little annual or diurnal temperature variation. *Usnea durietzii* is found at the lower altitudes (*c.* 3000–4000 m) and is characteristic of dry, exposed, rocky páramos in communities associated with *U. acanthella, U. bogotensis*, and *Stereocaulon* species, whilst *U. sphacelata* is confined to higher, alpine habitats.

Biogeography

Many authors (Ahmadjian, 1970; Dodge, 1965*a*; Filson, 1982; Jørgensen, pers. comm.; Lamb, 1970) regard the antarctic lichen flora as a mixture of relict endemic elements, which survived Pleistocene glaciations, as well as immigrant elements that recolonised the continent from adjacent areas, for example Fuegia. Lindsay (1977*a*) considered the nunatak cryptogamic flora of Antarctica was, in contrast to the arctic, somewhat impoverished as a result of polar isolation, more drastic climatic changes during the late Cenozoic, and slower rate of recolonisation. However, despite physiographical, climatic, and vegetational differences between the polar regions, taken in its entirety, the present-day lichen flora of Antarctica is as rich as that of the arctic, thus indicating a varied origin and opportunities for speciation.

The present day distribution of the subgenus *Neuropogon* has often been used as an example by biogeographers when discussing origins of bipolar disjunctions. Together with other genera which have a predominately southern hemisphere distribution, for example *Menegazzia, Placopsis,* and *Pseudocyphellaria,* it has been generally accepted (Du Rietz, 1929, 1940; Galloway, 1979; Henssen & Jahns, 1973; James, 1960; Lindsay, 1977*a*; Lynge, 1938, 1941) that the subgenus *Neuropogon* possibly had a monophyletic southern origin. However, many features are shared with the subgenus *Usnea*, for example pigmentation of pseudoisidia, and this could indicate either common ancestry or subsequent parallel development. This contrasts with other genera, for example *Bryoria* and *Evernia*, which are thought to have evolved in the northern hemisphere, since they are today poorly represented or absent in the southern hemisphere (Galloway, 1979).

Jørgensen (1983) postulates that the present-day tricentric antarctic distribution of fertile species, as exemplified by *Usnea aurantiaco-atra* in southern South America–Antarctic Peninsula, *U. ciliata* in New Zealand, and *U. taylorii* in the subantarctic Indian Ocean, indicates ancient antarctic origins. This is despite difficulties in associating a cold-tolerant group with Gondwanaland when glaciation only occurred comparatively recently. A possible centre for subsequent speciation may have been in South America–west Antarctica, but Jørgensen proposes that some elements must have been present in Gondwanaland to account for present-day distributions.

Krog (1982) considered that disjunct distributions of several genera in the Parmeliaceae could indicate origins in the Cretaceous or Late Jurassic. Present-day distributions of fertile *Neuropogon* species indicate that the subgenus may have been established in Gondwanaland prior to the opening up of the south Atlantic at the start of the Cretaceous (Raven & Axelrod, 1974). The asexual species *Usnea patagonica*, which occurs in Patagonia and possibly South Africa, may represent the remnants of a once much richer flora in South Africa that was subsequently wiped out. However, distributions based on asexual species are likely to be speculative in view of the likelihood of subsequent long-distance dispersal.

Krog (1982) also suggested that the distribution of *Neuropogon* is an indication that the subgenus is more primitive than the more widespread and diverse subgenus *Usnea*. Today *Usnea s. str.* is mainly a tropical genus with only a few, all asexual, species sharing the same habitats with *Neuropogon*. This distribution indicates that *Usnea* may be a much younger group and any connection between the two subgenera must be very ancient. Certainly some of the South American species included in the subgenus, for example, *Usnea durietzii* and *U. patagonica*, have close affinities with the subgenus *Usnea* which are discussed under 'Generic concept'. (p. 42). These species might either suggest evolution from *Neuropogon* to *Usnea* or convergent evolution, or represent remnants of an ancestral group from which *Neuropogon s. str.* adapted to tolerate polar environments and *Usnea* spread to occupy a wider range of habitats and less severe ecological conditions. Similarly, one species, *U. neuropogonoides*, has some affinities with *Protousnea* although the two groups differ in other respects, including chemistry. *Protousnea* appears to be a further modification of the basic *Usnea*-type, and may be regarded (Krog, 1976) as a rather primitive group with possible affinities with hypothetical predecessors.

The unique thallus anatomy of *Usnea taylorii* might be interpreted as an indication of a primitive species, but is more likely to have been secondarily derived from a species with a thick axis, for example *U. aurantiaco-atra*. This species is confined to the Îles Kerguelen, Heard Island, and Îles Crozet. There is geological evidence (Brundin, 1970; Harrington, 1965) that these islands are partly ancient and partly of recent volcanic origin; thus indicating a Gondwanaland connection with an ancient endemic flora (Dodge, 1948). Biogeographically these islands, with Marion and Prince Edward Islands, form the Kerguelen Province (van Zinderen Bakker, 1971).

There is evidence that the so-called 'Grande Terre' of the Îles Kerguelen, which straddles the Antarctic Convergence, had an aberrant type of glaciation with certain sheltered areas probably serving as refugia for flora and fauna during the glaciations (van Zinderen Bakker, 1970). A parallel may be drawn from studies on an endemic genus of chironimid midges found on Îles Crozet (Brundin, 1970) which are thought to be the survivor of a group whose ancestors existed during the Jurassic–Cretaceous transition. This would indicate that such islands must have been isolated before the separation of Antarctica, New Zealand, and Australia, and like Îles Kerguelen and Heard Island are thought to be of continental origin (Shields, 1976).

The bicentric distribution of *Usnea trachycarpa* in Patagonia with the Falkland Islands and Îles Kerguelen suggests that this could be a very old species with origins in Gondwanaland, since it is unlikely to have subsequently spread by long distance dispersal. The Falkland Islands are thought to have Precambrian origins (Shields, 1976). Even as early as 1879 Hooker (Hooker, 1879*a*) recognised affinities between the vascular and cryptogamic floras of Îles Kerguelen and South America.

This is in contrast to the much younger subantarctic islands that were of recent volcanic origin, for example Marion and Prince Edward Islands, which were also subsequently glaciated (van Zinderen Bakker, 1970; Verwoerd, 1971). Despite the previous acceptance of an endemic sorediate species of *Neuropogon*, *Usnea insularis* (= *U. antarctica*) (Dodge, 1948; Lamb, 1939*a*; Lindsay, 1977*b*) it is consequently unlikely that such a species could have had sufficient time to evolve. It is more plausible that *U. antarctica* recolonised these islands post-glacially by long distance dispersal via the Scotia Arc, which is probably of continental origin, or with islands dating from Precambrian to Cretaceous times (Shields, 1976). Lindsay (1977*b*) indicates that the lichen flora of the Prince Edward Island group has affinities with that of the Îles Kerguelen, as exemplified by *Orceolina kerguelensis*, which has recently been found on Îles Crozet (*Tilman*, BM). However, these islands floras also share a common bipolar element.

Bouvetøy and the other islands of the Scotia Arc, which extends eastwards from Tierra del Fuego through South Georgia to the South Sandwich Islands then westwards through the South Orkneys towards the Antarctic peninsula (Greene, 1964), were similarily glaciated and consequently have a low incidence of endemism. Two main species, *Usnea antarctica* and *U. aurantiaco-atra* have recolonised these islands from Fuegia, and Bouvetøy represents the easterly limit of the latter species. Some ice-free nunataks may have existed along the Scotia Arc, although there is, as yet, no geological evidence, where *U. antarctica* and *U. aurantiaco-atra* may have survived glaciations (Lindsay, 1975). The South Sandwich Islands are of recent origin, formed from a crust *c.* 8 million years old, and have no exposed rocks older than *c.* 3 million years and are still actively volcanic. Consequently the flora must have arrived by transoceanic migration (Longton & Holdgate, 1979).

Biogeographers attach considerable importance to the extent of endemism, particularly at species level, in a given area. Results are often conflicting and may, in some instances, be more relevant for phanerogams. With lichens it is essential for the flora of a particular region to be well documented and compared to that of adjacent areas. The flora of the antarctic regions is a test case where failure to do this can lead to recording of spurious endemism, as, for example, in the case of the taxa described by Dodge (1965*a*, 1970). Many groups still require critical systematic revision, which may show that many endemic taxa are superfluous, merely representing environmental modifications rather than genetic differences (Filson, 1982).

Geological evidence (Harrington, 1965) indicates that east and west Antarctica had different origins, with the western, younger part having close affinities with South America. The islands of the northern Antarctic peninsula are thought to have Middle Paleozoic origins (Shields, 1976). Dodge (1948, 1965*b*, 1973) recognised endemic species of *Neuropogon* in east Antarctica derived from *Usnea antarctica*. Although this area is older, with Gondwanaland origins, such elements are now regarded as ecotypes (Ahmadjian, 1970). Their precursors may have survived Pleistocene glaciations on inland nunataks or ice-free refugia (Lamb, 1970) and subsequently spread along melt-water channels to colonise coastal areas (Filson, 1982). However there would not have been sufficient time for speciation to occur, since the rate of evolution in lichens is thought to be very slow (Lindsay, 1977*a*; Jørgensen, 1983) and then growth is even slower in polar regions (Lamb, 1970). This is in contrast to the proposed relict indigenous elements which may have survived at high altitudes above the tree-line during more temperate eras and form the truly endemic portion of the flora.

The Antarctic peninsula is considered (Dodge, 1973; Lindsay, 1977*a*) to have a high incidence of specific, but low generic, endemism. This is exemplified by the occurrence of lichen groups which have developed unusual characteristics such as the possibly more highly evolved stipate forms of many crustose genera (Lamb, 1970). Many of these species also occur in southernmost South America, having a distribution pattern similar to that of *Usnea aurantiaco-atra* and *U. subantarctica*. Such species probably evolved during the rapid phase of speciation that occurred in Patagonia after the initial break up of Gondwanaland, and spread postglacially into the Antarctic peninsula via the Scotia Arc. Limited dispersal of fertile species must have occurred by this route although the Arc was formed after the separation of the Antarctic peninsula and South America. The timing of the separation of the Antarctic peninsula is uncertain but an estimate of 29·3 million years B.P. is preferred by Crook (1981). Dodge (1973) recognised a greater number of *Neuropogon* species in the Antarctic peninsula than are accepted here. At present five, or possibly six, species are known, of which none are endemic. In contrast ten species occur in Fuegia, of which one fertile species, *U. perpusilla*, is endemic, and one, *U. aurantiaco-atra*, is common to the Antarctic peninsula and islands.

It is clear from present-day distributions that there has at some stage been explosive speciation of *Neuropogon* in southernmost South America and subsequent spread, possibly as a response to drastic climatic changes (van Zinderen Bakker, 1970) and opening up of ecological possibilities. This does not necessarily prove that the area coincides with a centre of origin and could conversely be regarded as an area where many species occur as the result of continual replacement or accumulation of relicts (Darlington, 1965). There is evidence that the greater part of Tierra del Fuego was glaciated although refugia may still have existed for old species, such as *U. trachycarpa*. Other species, such as *U. antarctica*, may have evolved from a fertile primary species, i.e. *U. aurantiaco-atra*, and subsequently spread postglacially by long distance dispersal.

South America has long been of biogeographical interest as a centre of speciation and a migration route to and from the northern hemisphere. With respect to *Neuropogon*, it is apparent that at some stage taxa were isolated in the northern Andes. Such proximity to the tropics and varied climates has led to the evolution of a series of closely related, asexual species, such as *Usnea acanthella* and *U. durietzii*, which together with *U. sphacelata* are often difficult to identify and may indicate either a centre of great diversification or parallel evolution.

Only one of these asexual, South American taxa managed to spread into North America. *Usnea sphacelata* probably had its origins in Patagonia since it may be the sorediate counterpart of *U. perpusilla*. Various theories as to how and when this migration occurred have been proposed or discussed by previous authors (Du Rietz, 1929, 1940; Lynge, 1941). It seems probable that migration north may have occurred prior to the recent joining of North and South America; possibly along a series of volcanic islands during the Late Cretaceous (Raven & Axelrod, 1974; Jørgensen, pers. comm.). The absence of a possible fertile counterpart in the northern hemisphere and the uniformity of the population in contrast to the greater variation found amongst southern hemisphere populations indicate recent migration to the northern hemisphere. A similar situation is seen in *Placopsis* and *Menegazzia*. However, it might be argued that less variation is found because climatic conditions have been more stable than in Antarctica during the late Cenozoic glaciations and the arctic was not isolated geographically (Lindsay, 1977*a*). Spread in the northern hemisphere was apparently eastward towards Greenland, following the prevailing winds, rather than across the Bering Straits. The distribution of *U. sphacelata* is not truly circumpolar and is mainly in the Canadian eastern arctic, being rare between Novaya Zemlya and western arctic Canada, with a single record from the New Siberian Islands (Lynge, 1941). Thomson (1972) considered that the present day disjunct distributions of many arctic lichens may reflect the availability of suitable habitats rather than the spread from a centre of origin. Since *U. sphacelata* is more or less confined to island groups in the northern hemisphere rather than the continents, this might be a relevant proposition. Post-Pleistocene colonisation was probably rapid from North America by means of wind-blown propagules and thallus fragments.

Biogeographic treatments of New Zealand have been the subject of much debate and were recently summarised by Craw (1978). Galloway (1979) comments that the cryptogamic and phanerogamic floras of New Zealand and southern South America have many common genera but few shared species. For example, in *Usnea* subgenus *Usnea* closely related species occupy similar habitats. *U. xanthopoga* and *U. contexta* are replaced by *U. nobilis* and *U. pallida* in South America (Galloway, 1979) and also *U. torulosa* and *U. inermis* by *U. igniaria* and *U. nidulifera*. Similarly different fertile species of *Neuropogon* also occur. This is also true for *Menegazzia* where few species are common to South America and New Zealand (P. W. James, pers. comm.). In the New Zealand alpine flora there is a considerable extent of endemism in phanerogams but this is not as high in the lichen flora.

New Zealand was separated from Gondwanaland, and hence from Australia and Tasmania, approximately 80 million years B.P. (Raven & Axelrod, 1974), whilst separation of Australia and Antarctica did not occur until 60–53 million years B.P. (Crook, 1981). The subgenus *Neuropogon* is restricted to schists east of the main divide in the South Island and is rare in the North Island. This substrate specificity could indicate that a norstictic acid-containing precursor of the *Usnea ciliata* aggregate or even *U. ciliata* itself, was isolated at that time and subsequently underwent speciation with the resulting four taxa. This isolation occurred well before the more or less direct migration route between South America and Australia via Antarctica was broken, and hence explains why one would not expect *U. ciliata* to occur in South America, despite erroneous reports (Lamb, 1948*a*). In South America *U. ciliata* is replaced by *U. aurantiaco-atra* and *U. perpusilla*.

The lichen flora of Australia has diverse origins (Rogers & Stevens, 1981) but how and when *Neuropogon* reached Tasmania and Victoria remains conjectural. As far as vascular plant dispersal is concerned there have been conflicting views as to whether migration was possible from east to west (Wardle, 1978) as well as from Tasmania to New Zealand with the prevailing winds (Raven, 1973). The former migration would had to have occurred if *Neuropogon* spread to Tasmania after separation of New Zealand. Evidence that this direction of migration has occurred in some groups of organisms is also given by Fleming (1976). An alternative explanation is that ancestors of *Usnea ciliata* were much more widespread in Gondwanaland and consequently already present in Tasmania and New Zealand prior to continental movements; this certainly seems to be true for species of *Menegazzia* (P. W. James, pers. comm.). Additional evidence for spread from New Zealand comes from the fact that *U. ciliata* has not reliably been recorded from Tasmania and the two species present, *U. acromelana* and *U. subcapillaris* could spread by soredia or thallus fragmentation.

Slight differences between New Zealand and some Australian populations may either be due to ecological conditions or conversely indicative of a longer isolation. Long distance dispersal may have also been by other agents, including birds (Bailey & James, 1979). There is evidence (Burton, 1968) that gulls and skuas use lichens to line their nests. In addition, Wardle (1978) suggested that dispersal of sorediate taxa may have still occurred from Antarctica to New Zealand prior to glaciation. This may account for the presence of an antarctic element, *Usnea antarctica* and *U. sphacelata*, in the flora. It seems more probable that *U. sphacelata*, from its restricted distribution on very old outcrops, is a relict species. Further evidence also comes from the recent discovery of this species in north-west Nelson (herb. Bartlett 25810!, 25811!), together with other bipolar species including *Solorina spongiosa* (Galloway, pers. comm.). In contrast *U. antarctica* may have spread more recently from Fuegia or Antarctica.

The sorediate *Usnea acromelana* is common in Australasia and infrequent in southernmost South America and the Antarctic peninsula area. It may be argued that this species subsequently spread from Australasia, where its fertile counterpart, *U. ciliata*, occurs, to Patagonia via Antarctica before the continents finally separated. However, this present-day distribution does not necessarily reflect earlier patterns and migration might have occurred in the opposite direction, although *U. ciliata* is today confined to Australasia. *U. acromelana* is absent from east Antarctica and associated subantarctic islands which may be a result of ecological factors, with habitats more suited to *U. antarctica* and *U. sphacelata*. It is also worth emphasising that some populations from the Antarctic peninsula and Patagonia are only tentatively included in *U. acromelana* and may eventually prove to be examples of parallel evolution. Ecological factors may also explain the limited distribution of *U. subantarctica*.

Fleming (1976) considered that most of the outlying subantarctic islands of New Zealand were not connected to the mainland during the Tertiary, being partly formed during that era by volcanism although with older, continental elements (Shields, 1976). He suggested that they were subsequently glaciated or had very cold climates with the result that many inhabitants are more recent colonists. However, Wardle (1978) drew attention to the high level of endemism in the vascular plant flora on the Antipodes, Stewart, Campbell, and Auckland Islands, which suggests they survived glaciations; on the other hand there is evidence that the Macquarie Island flora was to some extent impoverished by glaciations (van Zinderen Bakker, 1970).

Dodge (1973) believed that there was no relationship between the antarctic lichen flora and that of Îles Kerguelen and the subantarctic islands of New Zealand. However, it has now been shown that the New Zealand flora has a substantial austral element (Galloway, 1979) which has affinities with those of its subantarctic islands (Dodge, 1970) and even with Îles Kerguelen, as illustrated by the distribution of the genus *Steinera* (Henssen & James, 1982) which is probably a relict of a once more widely dispersed flora lost from New Zealand and South America during glaciations (Galloway, 1979). The oceanic climate of Auckland and Campbell Islands is not suitable for *Neuropogon* species. It is probable that *Usnea acromelana* spread to Chatham Island from New Zealand, and *U. antarctica* to Macquarie Island, by later, long distance dispersal.

The distribution and evolution of chemical races in *Neuropogon* has not been considered from a biogeographical standpoint. However, it does seem likely that the precursor of the subgenus might have contained norstictic acid, since this substance is the most widely distributed, with subsequent development of other races. Alternatively, many species, including *U. taylorii*, often lack medullary substances; a state that is the commoner phase of many antarctic species.

Discussion

Circumscription of the species

The genus *Usnea s. lat.* is notorious when it comes to delimiting species since there is inherent a great plasticity of form. The subgenus *Neuropogon* is no exception. Complexes exist within which it may be difficult to delimit individual species because rare linking intermediates are encountered. Such groups of individuals are regarded as noda along an axis of variation and may either be considered as distinct species, if sufficient criteria exist, or else as variants of a single species. Often there are indications that convergent evolution has occurred and this may lead to misidentifications. Immature, damaged, or thalli from sites of ecological stress may prove anomalous or even impossible to identify.

In his world monograph Lamb (1939*a*) attached importance to both morphological and chemical characters when delimiting taxa. The morphological features found to be useful criteria are cortical features, relative widths of axis and medulla and corresponding laxness, and colour of the apothecial disc, and presence of rays. In asexual species the type and formation of propagules is important and may sometimes be species specific. For example, soralia may be plane, crateriform, ulcerose, or globose, and soredia may or may not be pigmented. In some instances the habit and branching of the thallus as well as the form of blackening of the holdfast may also be of value besides distributional and ecological considerations. Frequently, during this study, it has been found that a combination of characters must be taken into account when identifying a particular species. This accounts for the wide range of infraspecific variation and any anomalies that may consequently occur.

Microscopical characters, for example spores and conidia, have not been studied in depth and hence no great taxonomic value is attached to them in this instance, although they have belatedly been found to be significant in other instances within the Parmeliaceae (Krog, 1982). Lamb (1939*a*) suggested that the structure or formation of conidia may provide useful evidence for separating genera. This theory has been proved by recent authors (Culberson & Culberson, 1980; Krog, 1982; Hawksworth, 1981) who have found them useful in separating genera or species. Krog (1976) used pycnidial morphology to separate *Neuropogon* from *Protousnea* based on absence of pigment in the ostiole rather than details of conidia structure or formation. Pycnidia are rather rare in *Neuropogon*, although further work on conidial shape and formation may provide useful information in confirming conspecificity of taxa such as *Usnea aurantiaco-atra* and *U. melaxantha* (see ‘Morphology’ p. 11).

As mentioned earlier (p. 3) virtually all Lamb's taxonomic work on *Neuropogon* was carried out before the advent of TLC, relying on thallus spot tests and microchemical crystal tests. Consequently too much weight was sometimes placed on slight differences in concentration of medullary substances. The use of TLC in delimiting species is discussed below. In contrast Dodge (1948, 1973) virtually ignored chemical data and attached considerable weight to small differences in morphology and thallus anatomy. His very narrow species concepts led to the description of a large number of taxa which cannot be accepted today. Reasons for reducing many of these taxa to synonymy are also discussed under the relevant species.

From studying a wide range of material some indication has been obtained of the morphological variation of each species. Concepts may have to vary according to the species concerned, and a wider or narrower range of variation of a particular character accepted. Frequently a broader view must be taken of species which have a wider distribution. These are species which usually only spread by means of vegetative propagules. Such species may occupy a wider range of habitats or have a greater ecological tolerance and hence exhibit more variation than species with a limited range (Krog & Swinscow, 1981). Swinscow & Krog (1978) proposed the concept that widespread and variable *Usnea* species may be represented by different morphotypes or chemical races towards their distributional limits. At extremes such thalli may look very different and have often been interpreted as distinct species. Consequently several *Neuropogon* taxa accepted by previous authors are here reduced to synonymy (Table 5). An example is *Usnea sphacelata* where there are some differences between certain antarctic and arctic propulations, although this variation is not considered to be sufficient to warrant the acceptance of distinct taxa.

In addition there may be considerable variation within populations resulting from ecological factors (Filson, 1982, Hawksworth, 1973) which may be misinterpreted. It is possible that the diverse forms met with whilst evaluating the variation of *Usnea sphacelata*, particularly in South American and antarctic populations, are the result of the response to differing ecological conditions which some authors would recognise as distinct subspecies.

Hawksworth (1972) discussed the effect of ecological factors on species delimitation in lichens. He concluded that variations may be caused by phenotypic plasticity but in addition these may have a genetic origin and require taxonomic recognition. Hence, ideally, the need for careful field analysis before new taxa are recognised.

It is very likely that montane and arctic-alpine conditions influence variation in thallus morphology of fruticose lichens. Previous authors have come to different conclusions. For example, Kristinsson (1969) studied *Cetraria islandica* and *C. ericetorum* in Iceland and found no consistent correlation between morphotypes and chemotypes, finding a range of forms intermediate between the two taxa. More recent world-wide studies by Kärnefelt (1979) have revealed that the two *Cetraria* species may be further subdivided with geographical subspecies, using taxonomic and ecological criteria. Both species have a bipolar disjunction coinciding with racial differentiation and the recognition of a southern hemisphere subspecies for each. However, there are many examples where species, which have their main distribution in the northern hemisphere, and also occur in the southern hemisphere, do not develop a southern race, for example *Cladonia mitis* and *Alectoria nigricans* (Kärnefelt, 1979).

Usnea sphacelata could be regarded in a similar fashion as a series of subspecies. However, in many instances, as with *U. acromelana*, it seems more plausible that environmental factors are the primary cause of variation. Altitude may be important since thalli from high-altitude 'nunatak' situations are usually distinct, although these intergrade with lower altitude forms. Similarly, although the majority of southern hemisphere material of *U. sphacelata* examined is slightly different from that of the northern hemisphere, occasionally thalli 'true to type' do occur in populations of varied morphology. Depsidone-containing specimens belong to *U. subantarctica*.

Thalli in shaded conditions are greener than those in exposed situations due to lower concentrations of usnic acid. Parallels exist in the pigmentation of antarctic Teloschistaceae (Filson, 1969). In more exposed habitats thalli are often smaller, may be more richly branched, or become subdecumbent, or may be more extensively pigmented. The development of a violaceous black pigment in the outer layers of the cortex is thought to be a shielding mechanism against UV radiation. Lindsay (1977*a*) observed that in the continental antarctic, thalli of *Usnea sphacelata* are heavily or even almost entirely pigmented, whilst in the maritime antarctic (Antarctic peninsula) thalli are only lightly variegated at branch apices. Ecological factors may also effect the development of the lax medulla in some species, for example *U. perpusilla* and *U. sphacelata*. Such environmentally induced variation may account for some abnormalities that are occasionally encountered. These include the rare occurrence of minute papillae in species which usually have a smooth surface, for example, *U. acromelana* and *U. taylorii*, or the uncharacteristic presence or absence of excipular rays in fertile species.

Variation and development of atypical features in eastern antarctic populations of *U. antarctica* and *U. sphacelata* has led to the description and acceptance of many distinct taxa from this area by Dodge and his associates, who applied very narrow species concepts and recognised pockets and endemism around the eastern antarctic (Dodge, 1948, 1965*b*, 1973). Some of Dodge's taxa are difficult to assign to either *U. antarctica* or *U. sphacelata*, particularly where they are based on poorly developed thalli or when holotype material is not available for study. In addition named material examined of a single species often included both *U. antarctica* and *U. sphacelata*. For example, *U. subfoveolata* and *U. subpapillata* were both described from the same locality in Queen Mary Land. Type specimens were examined by Lamb (1964) and photographed (Lamb, unpublished notes, AAS!) and are probably referable to *U. antarctica*, although I have examined material from the type locality, also cited by Dodge, which belongs to *U. sphacelata*. Both species are present in collections identified as *U. subpapillata* in US. Similarly Dodge described a further two species from an adjacent locality in Queen Mary Land. *Usnea laxissima* is a decumbent form of *U. sphacelata*, whilst *U. pustulata* is synonymous with *U. antarctica*.

Occasionally, specimens from eastern Antarctica have been misidentified as *Usnea acromelana*, (for example, Golubkova & Schapiro 1970; Filson, 1975), although in Antarctica the species is confined to the Antarctic peninsula. Lamb (1939*a*) described two forms of *U. acromelana* from Antarctica which are now recognised as belonging to *U. sphacelata*. Sometimes specimens of *U. sphacelata* have a very smooth, slightly waxy, unpigmented surface and a somewhat compact medulla. These features, combined with the production of black nodular soralia, suggest some affinities with forms of *U. acromelana*, although specimens lack the blackened annulations and compact medulla that are features of that species.

The form of vegetative propagules is often species specific, but in rare instances there may be an intergradation between granular soredia, pseudoisidia, and true isidia, often with erosion and secondary regeneration. True isidia are only known in one species, *U. acanthella*, in *Neuropogon*. The formation of various propagules is discussed under 'Morphology' (p. 9). Examples include corticate outgrowths in soralia of *Usnea acromelana* and *U. antarctica* which may not be readily distinguished from the pseudoisidia of *U. durietzii* and *U. patagonica*. *U. patagonica* may be regarded as an intermediate species between *U. antarctica* and *U. durietzii* (Table 3). Some taxa are now regarded as conspecific which were originally distinguished on the form of the soralium; for example in *U. acromelana* and var. *decipiens* (Lamb, 1939*a*). If such distinctions are maintained this should only be at infraspecific level, although sometimes the range of variation can be observed within a single thallus.

In some instances it is difficult to distinguish asexually reproducing species where several species overlap in their distribution. This is generally the case in subantarctic South America (Patagonia) where *U. antarctica, U. acromelana, U. durietzii, U. patagonica, U. sphacelata*, and *U. subantarctica* are all known to occur. In addition the area is poorly collected. Frequently thalli examined are small or somewhat moribund and consequently have not developed sufficient features characteristic of a particular species. Many of the species are in the depsidone-deficient phase and so chemistry cannot be used as an additional guideline.

Where distributions overlap it is also likely that forms intermediate between species may occur. In addition species are reaching their distributional limits and as a result often produce atypical forms. In some instances altitude may have the same effect on the form of the species as latitude. Such a phenomenon is often observed in New Zealand populations of *U. acromelana* where thalli from lower altitudes may become discoloured and produce contorted or grotesque forms, often with proliferation of soralia to produce corticate outgrowths resembling pseudoisidia. In such instances the only species liable to cause confusion is *U. torulosa*.

Recent advances in microchemical techniques resulting in the identification of lichen substances, in particular the development of rapid methods of TLC, have led to differing opinions on the taxonomic status of chemical variants of a species. Some workers regard chemical variants as distinct species, although there are no morphological differences; others prefer to regard them as races of the single species concerned. A well-known example is the range of opinion concerning the *Ramalina siliquosa* complex which is summarised by Krog & James (1977). Whilst delimiting species within *Neuropogon* I have attempted, as with morphological variation, to evaluate each case of chemical variation individually, based on the study of a large amount of material. No taxonomic value is attached to accessory substances, for example UV + unknowns, which vary from abundance to absence within a given species. Similarly the occurrence of psoromic acid is rarely considered to be species specific, although it may rarely occur as a common denominator that unites morphologically uniform chemotypes, for example, in *Parmelia direagens* (Krog & Swinscow, 1981).

The chemistry of *Neuropogon* species is not as complex as in some other genera in the Parmeliaceae since most of the comparatively few depsidones and depsides that are known are closely related chemically. Chemical data have supported morphological evidence that *Usnea aurantiaco-atra* and *U. melaxantha* are conspecific. Thalli are occasionally found with a mixed chemistry in areas where the two depsidone-containing races overlap and cannot be distinguished morphologically or from depsidone deficient material. This is discussed more fully under *U. aurantiaco-atra* (p. 71) and is a further example of an instance of where extremes in variation were previously thought to represent distinct taxa. Various epithets have been applied to races of *U. aurantiaco-atra* at different times by previous authors and these are summarised in Table 4.

Chemical data, in some instances, may prove useful in the recognition of species groups and species pairs. The concept of a species pair: a fertile species and a derived asexual species, has been accepted or rejected by various authors, usually the former. Du Rietz (1924) proposed two types of clones based on extant or extinct primary species and this concept has been followed up by Hale (1965), Poelt (1970), Swinscow & Krog (1978), and Krog & Swinscow (1981). Poelt (1970) referred to a 'species pair' when both the fertile and asexual counterparts were known and to 'secondary species' where the primary species is unknown, as is frequently the case in some fruticose groups. In contrast, Tehler (1982, 1983) considers that secondary asexual taxa are best expressed as formae rather than as distinct species.

In *Neuropogon*, in the few instances where obvious species pairs occur, I prefer to regard the taxa as distinct species. Otherwise it would become increasingly difficult to delimit taxa at species level besides making allowances for the wide range of infraspecific variation and

Table 4 Epithets applied to chemical races of *Usnea aurantiaco-atra (Neuropogon aurantiaco-ater)* by major authors.

Author	norstictic/salazinic acid	fumarprotocetraric (±)
Motyka (1936–38)	*melaxantha* *aurantiaca*	*aurantiaco-atra* *fasciata* *strigulosa*
Lamb (1939*a*)	*melaxantha* *aurantiaca*	*aurantiaco-atra* *strigulosa*
Lamb (1948*a*)	*melaxantha*	*aurantiaco-atra*
Lamb (1964)	*aurantiaco-atra*	*fasciata*
Dodge (1973)	*aurantiaca* *melaxantha*	*aurantiaco-atra* *fasciata* *siplei* (?) *strigulosa*
Lindsay (1975)	*aurantiaco-atra*	*fasciata*

chemical variation that already occurs. The chemical races of *Usnea aurantiaco-atra* have already been mentioned above in the context of species delimitation. *U. antarctica*, from similarities in morphology and anatomy, is thought to be the asexual counterpart. In addition *U. antarctica* is sometimes found fruiting and also the same two depsidone-containing races as well as a depsidone-deficient race are known. The norstictic-salazinic acid race is extremely rare and is only known from a single collection from the centre of distribution of the corresponding race of *U. aurantiaco-atra*.

Similarly members of other species pairs may have more than one chemotype with no obvious morphological differences. Such chemotypes are regarded as races rather than distinct taxa. Either the primary or derived species may exhibit more than one chemical race. Examples exist in the *Usnea ciliata* complex which consists of four species dominated by norstictic acid and salazinic acid containing thalli. *U. acromelana* is without doubt the sorediate counterpart of *U. ciliata*, sharing a range of morphological features including a waxy, annulate surface, a compact medulla, and, when fertile, apothecia with rays and a blackened disc. In Australasia the two species overlap and only one chemical race, with norstictic and salazinic acids, is usually encountered; depsidone deficient material of *U. acromelana* is confined to a single locality in Victoria. *U. acromelana* has a more widespread distribution and is a rare species in southernmost South America, the Antarctic peninsula and islands. Within this South American–antarctic distribution three chemical races are known: (1) norstictic acid and salazinic acid, (2) psoromic acid, (3) depsidone deficient, indicating greater diversity at distributional limits. Two other Australasian species, *U. subcapillaris* and *U. pseudocapillaris*, belong to the complex and are derived from *U. ciliata* and *U. acromelana* respectively. Conversely only a norstictic-salazinic acid race is known in *U. pseudocapillaris* whilst three morphologically uniform chemical races occur in *U. subcapillaris*: (1) norstictic acid and salazinic acid, (2) squamatic acid ± hypothamnolic acid, (3) psoromic acid. Races 2 and 3 have a more limited distribution and occasional thalli with mixed chemistry are known. The origin of race 2 is particularly intriguing since these substances do not occur in any other species in *Neuropogon*.

Amongst the remaining species it is not so easy to pinpoint close relationships. There is often not sufficient evidence to indicate species pairs and also more asexual species exist than possible fertile, primary counterparts. *Usnea sphacelata* and *U. perpusilla* possibly form a species pair, based on the range of morphological and anatomical variation found in both species. Both species lack a depsidone-containing race, apart from the freak occurrence of psoromic acid. Specimens previously included in *U. sphacelata*, containing norstictic acid and/or salazinic acid, are here included in *U. subantarctica*; a species also separated on morphological and distributional features. The distinction of *U. subantarctica* as a species from *U. sphacelata* might be considered to be rather tenuous, particularly in the depsidone-deficient phase. However, the rare occurrence of fertile material indicates other affinities which do not fall into the possible concept of an *U. perpusilla–U. sphacelata* species pair. The discovery of fertile *U. sphacelata* with the '*perpusilla*' type of apothecia would finally settle this dilemma.

The existence of a sorediate counterpart to *Usnea trachycarpa* remains uncertain, although two possible candidates exist: *U. patagonica* is often found in the same habitat in South America but has fewer fibrils, more or less delimited, blackened holdfast, is not known to contain depsidones (i.e. norstictic acid), but does contain the same or similar fatty acids as often occur in *U. trachycarpa*. The other, more likely, possibility is *U. subantarctica* which again is less fibrillate, more extensively pigmented, has '*trachycarpa*' type of apothecia, often contains norstictic acid and/or salazinic acid, but lacks the fatty acids. It is possible that the sterile *U. neuropogonoides* may be derived from *U. trachycarpa*, but they do not represent a species pair.

Lamb (1939*a*) described the sorediate *Usnea insularis* from Marion Island and indicated that the species may have closest affinities to *U. taylorii*. However, *U. insularis* is here reduced to synonymy with *U. antarctica* on the basis of morphology, anatomy, and the presence of fumarprotocetraric acid, a depsidone that is extremely rare in *U. taylorii*. Further collections may reveal an asexual counterpart to *U. taylorii*.

Generic concept and infrageneric classification

The genus *Usnea s. lat.* has been divided into various genera or subgenera of which three, *Neuropogon, Protousnea,* and *Lethariella,* are frequently accepted as distinct genera. Other genera, for example *Parmelia*, have been subjected to a similar chequered existance and their delimitation may eventually rest on critical study of, for example, pycnidia, which are being found to be of value in delimitation of some orders, genera, and species (Krog, 1982; Hawksworth, pers. comm.). Meanwhile distinctions between neighbouring genera may remain somewhat obscure. This is particularly true of *Neuropogon* where some authors have accepted the group as a distinct genus, others as a subgenus of *Usnea*; two authors (Jatta, 1900, 1909; Lamb, 1939*a*, 1964) changed their opinion. The main arguments have centered around whether thallus colour and pigmentation, disc colour, saxicolous habitat, and restricted distribution are sufficient criteria for separation at generic or subgeneric level.

Previous authors have interpreted *Neuropogon* in various ways. Jatta's concept (1900) was based on two species that are now excluded from the subgenus. Du Rietz (1926) separated the subgenus from *Usnea* solely on the basis of apothecial disc colour and consequently had a much broader concept of *Neuropogon* than subsequent taxonomists. Eight out of the 13 species he included in his subgenus are now included in *Lethariella* and *Protousnea* (Krog, 1976).

Motyka (1947) accepted *Neuropogon* as one of six subgenera of *Usnea* on the basis that there were not sufficient distinguishing characters to warrant generic status. Motyka (1936–38) further subdivided the subgenus into three sections: *Sulphureae, Melaxanthae* and *Trachycarpae*, grouping the species according to shared characteristics. All Motyka's species are still included within the subgenus today, although six taxa (five species and one variety) have subsequently been reduced to synonymy. Two species, *Usnea durietzii* and *U. neuropogonoides*, were described by Motyka (1936–38) and placed in sections *Glabratae* and *Foveatae* of the subgenus *Euusnea* respectively. These species, as pointed out by Motyka, have many *Neuropogon*-type features and are here included in the subgenus for the first time.

Both Lamb (1939*a*, 1948*a*) and Motyka (1936–38) may be regarded as having a more conservative view of *Neuropogon* which will here be termed *Neuropogon s. str.* Dodge (1948) based his infrageneric classification on that of Motyka and accepted *Neuropogon* as a subgenus. In addition Dodge (1948, 1973) excluded five taxa from the subgenus and instead placed them in section *Laevigatae*, subsection *Roccellinae* of the subgenus *Euusnea* (i.e. *Usnea s. str.*) based on differences in the phycobiont. These taxa, all from the subantarctic islands of the southern Indian Ocean, were *Usnea taylorii* and four species that are here regarded as synonymous with *U. antarctica*. However, Dodge did consider these taxa to be somewhat intermediate between the two subdivisions and included them in the keys to both groups. A summary of the major taxonomic treatments is given in Table 5.

Recently there has been a tendency by many lichenologists to accept at generic level subdivisions of established genera often based on detailed anatomical studies. For example, Brodo & Hawksworth (1977), using SEM showed that differences exist in the cortex structure in *Alectoria s. lat.* and used this as additional evidence to segregate genera. The SEM was used here to compare *Usnea s. str.* with *Neuropogon* and no anatomical differences were found. Results also compared favourably with previously published SEM work on *Usnea s. str.* (López-Figueras & Palacios-Prü, 1981).

Some examples of instances where *Neuropogon* has been given generic status include Krog (1976, 1982), Galloway (1983, 1984), and Rogers (1981). Krog (1976) compared *Neuropogon* with *Protousnea* and listed a series of characters that could be used to distinguish the two genera. This may be an acceptable separation since there are many differences, including surface ornamentation, medullary chemistry, and habitat. Krog (1982) accepted six usneoid genera: *Neuropogon, Usnea, Protousnea, Evernia, Letharia,* and *Lethariella,* using colour and pruinosity of the apothecial disc as distinguishing criteria. She also proposed a hypothetical relationship in which *Protousnea* is more closely related to *Evernia* than to *Usnea* and *Neuropogon*.

Following Krog's classification the main difference between *Usnea* and *Neuropogon* lies in apothecial pigmentation and pruinosity. This is a much more acceptable distinction since, as will

Table 5 Examples of generic and infrageneric classification of *Neuropogon*.

Source	Classification	A	B
Nees & Flotow (1835)	Genus *Neuropogon*	2	1
Jatta (1900)	Subgenus *Neuropogon*	2	0
Du Rietz (1926)	Subgenus *Neuropogon*	13	5
Motyka (1936–38)	Subgenus *Neuropogon*		
	sect. *Sulphureae*	2	2
	sect. *Melaxanthae*	9	4
	sect. *Trachycarpae*	1	1
	Subgenus *Euusnea*		
	sect. *Foveatae*	0	1
	sect. *Glabratae*		
	subsect. *Pycnocladae*	0	1
Lamb (1939*a* & 1948*a*)	Subgenus *Neuropogon*	11	9*
Lamb (1964)	Subgenus *Neuropogon*	15	9
Dodge (1948 & 1973)	Subgenus *Neuropogon*	25	5
	Subgenus *Euusnea*		
	sect. *Laevigatae*		
	subsect. *Roccellinae*	5	2
Walker (present study)	Subgenus *Neuropogon*	15	15

Column A represents the number of species included in *Neuropogon* by the given author. Column B represents the number of species accepted here; * = one variety raised to specific rank. Where dates are combined, numbers of species are totalled.

become clear from this study, other criteria such as thallus colour and pigmentation (see below) and habitat may not be so reliable. However, even apothecial characters may not fit generic divisions. Krog (1976, 1982) gives examples of species included in *Usnea s. str.* which have flesh coloured to brown epruinose apothecial discs and therefore have close affinities to *Protousnea*, possibly representing an intermediate or primitive group. Consequently I prefer to follow the classification established by Henssen & Jahns (1973) and regard *Neuropogon* as a subgenus of *Usnea*.

It has become apparent from this study that *Neuropogon* has often been loosely defined and frequently used as a term of convenience when applied, in particular, to antarctic taxa. If only species confined to the arctic and antarctic were considered (cf. Lamb, 1964; Dodge, 1973) there would probably be sufficient character differences to favour generic status – namely thallus colour and pigmentation, a saxicolous habitat, and limited distribution – thus conforming to *Neuropogon s. str.* However, when subantarctic and, particularly, South American taxa and allied species are studied it is clear that the delimitation between *Neuropogon* and *Usnea* is often rather obscure. Several South American taxa are included here in the subgenus because they share many characteristic features. Since apothecia in these are unknown at present, and hence disc colour and pruinosity, their true systematic position cannot be ascertained.

The species that may be regarded as belonging to *Neuropogon s. lat.* are *Usnea acanthella, U. durietzii, U. neuropogonoides,* and *U. patagonica*. The high Andean species *U. acanthella* was included in *Neuropogon* by Lamb (1939*a*) and described as a form of *U. sphacelata* (as *U. sulphurea*). The variable extent of pigmentation and affinities to *U. durietzii*, combined with a wider substrate range, may indicate that *U. acanthella* is somewhat intermediate between the subgenera *Usnea* and *Neuropogon*. It is possible that the development of pigmentation may have arisen independently in different groups in response to harsh, exposed environments. A parallel may be found in the development of pigment in the genus *Ramalina*. *R. tigrina* is a terricolous species from the mist or fog zone of the Atacama desert in Chile (Follmann, 1966) and is characterised by a yellow-green thallus with prominent bands of black pigment.

Development of pigment is also variable in the genus *Alectoria*; for example apices of *Alectoria sarmentosa* ssp. *sarmentosa* may be occasionally striately blackened (Hawksworth, 1972).

Usnea durietzii occurs throughout the Andean chain, occasionally occupying the same habitats as *Neuropogon s. str.* Thallus colour is the same green-yellow as *U. acanthella* and similarly thalli do not become as straminous or fuscous in herbaria as *Neuropogon s. str. U. neuropogonoides* is only known from a few aged collections and is a scrambling, sometimes terricolous, species from Patagonia. Thalli are sterile, and may have affinities with *U. trachycarpa*. Similarly *U. patagonica* has limited pigmentation and shares common characteristics with *U. antarctica* and *U. durietzii*, the former species being accepted in *Neuropogon s. str.* It could also be argued that the two species, *U. subantarctica* and *U. trachycarpa*, which have red-brown to brown rather than black epruinose apothecial discs, might form a separate grouping or lie somewhere between *Neuropogon s. str.* and *s. lat. U. trachycarpa* is often scantily pigmented and has a subantarctic distribution whilst *U. patagonica*, a sorediate species that is rarely fertile, is more characteristic of *Neuropogon s. str.* and primarily has an antarctic distribution.

If thallus pigmentation and saxicolous habitat were used as the main criteria for segregating *Neuropogon* many other species belonging to *Usnea s. str.* which exhibit some pigmentation would have to be included. However, a distinction has to be drawn at some point otherwise the delimitation of the group would become much more obscure. These species are excluded from *Neuropogon s. lat.* and, although occasionally sharing the same habitat, are either rarely pigmented or have pigmentation confined to apices or isidia. Three examples are given in Appendix I.

Finally, thallus anatomy is sometimes used as a character for separating usneoid subgenera. The only *Neuropogon* species with a unique structure is *Usnea taylorii* in which the broad axis is invaded by medullary tissue, frequently resulting in sub-division or the formation of separate axial strands. In other species, for example *U. antarctica* and *U. aurantiaco-atra*, occasionally a small central cavity occurs in the axis without any significant penetration of medullary tissue or resultant segmentation. Dodge (1948) reported sub-divided axes in three *Neuropogon* species within the *Roccellinae*, although this only appears to be a constant feature of *U. taylorii*. Krog (1976) suggested that the axis of *Neuropogon* is most closely allied to that of *Usnea* subgenus *Eumitria* in which the axis is either tubular with a central cavity or is sometimes solid with a few longitudinal fissures (Swinscow & Krog, 1974). Krog (1976) also indicated similarities between the axes of *Neuropogon* and *Letharella* subgenus *Letharella*.

The subgenus *Neuropogon*

Usnea subgenus **Neuropogon** (Nees & Flotow, emend Nyl.) Jatta

Sylloge lichenum italicorum: 54 (1900). – *Neuropogon* Nees & Flotow in *Linnaea* **9**: 496 (1835). – *Neuropogon* Nees & Flotow, emend Nyl., *Synopsis methodica lichenum* **1**: 272 (1860). Lectotype: *Neuropogon antennarius* Nees & Flotow (see Taxonomic review – p. 4).

Description: Thallus fruticose, saxicolous, exceptionally terricolous or lignicolous, arising either from a small, delimited, or a broadly proliferating, basal holdfast, erect or subdecumbent, monopodial to ± subdichotomous or irregular, richly branched above, with or without short, lateral fibrils or numerous, attenuated secondary branches. Branches greenish yellow, becoming yellow or orange-brown on storage, ± variegated with violaceous black or black pigmentation, especially towards the apices. Branches terete, or rarely angular, in transverse section. *Surface* smooth or sometimes becoming faveolate, shining-waxy or matt, pigmented-annulate or minutely scabrid, sometimes papillate to verrucose-rugose; rarely maculate. *Cyphellae* and *pseudocyphellae* absent. In section of three distinct zones; cortex, medulla, and axis. *Cortex* variable in thickness, (50)–100(–200) μm, of indistinct, strongly gelatinised pseudoparanchyma, sometimes forming a pallisade-like layer towards the exterior. *Medulla* compact, lax, or sublax, of interwoven unorientated hyphae. *Photobiont*: coccoid Chlorophyceae, forming a ± continuous layer underlying the cortex. *Axis* chondroid, rigid, occupying 0·2–0·7(–0·9) of the branch diameter, cylindrical or slightly irregular, entire, very rarely sub-divided, of strongly gelatinised longitudinal, fastigiate, paraplectenchymatous hyphae. *Isidia* rare; *pseudoisidia* and *soredia* often present. *Apothecia* lecanorine, subterminal or lateral, subsessile to geniculate, with or without a subtending spur. *Disc* black, rarely rufous brown, matt or subnitid, epruinose. *Thalline excipulum* concolorous with the thallus, smooth, faveolate, scabrid or verrucose-papillate, with or without numerous, marginal, ± pigmented rays. *Thecium* 60–75 μm tall; *epithecium* aeruginose black or rarely brown, *hymenium* colourless below, blue-green or rarely brown above; *hypothecium* colourless to pale yellow. *Asci* clavate, *c.* 45 × 16 μm, tholus amyloid (I + blue); *ascospores* 8 per ascus, simple, hyaline, ellipsoid, 7–10(–12) × 5–7 μm, thick-walled (*c.* 1 μm). *Paraphyses* capitate, simple or branched, conglutinate. *Pycnidia* rare, pigmented, immersed in terminal branches; *conidia* sublageniform to filiform, 9–11(–14) × 1–1·7(–2) μm. *Chemistry:* depsides, depsidones, fatty acids, UV + unknowns, usnic acid. *Distribution:* polar alpine, predominately southern hemisphere, one species also northern hemisphere.

Key to the species

1a Soredia or isidia absent, apothecia usually present 2
1b Soredia or isidia present, apothecia rare 13

2a (1a) Apothecia absent, thallus straggling or apices capillaceous, or ± decumbent. (For erect, sterile, juvenile thalli see 2b) 3
2b Apothecia present, thallus usually erect, tufted 5

3a (2a) Thallus prostrate, scrambling. Main branches ornamented, rarely entirely smooth, not waxy, without black-edged annulations. Pigmentation scant. Medullary chemistry various, fumarprotocetraric acid sometimes present. Patagonia, Antarctic islands...... 4
3b Thallus subdecumbent with numerous extended, capillaceous, pigmented secondary branches. Main branches smooth, waxy, with black-edged annulations. Medullary chemistry various, never containing fumarprotocetraric acid. Australasia .... **13. U. subcapillaris** (p. 104)

4a (3a) Axis broad, greater than half branch diameter. Surface strongly verrucose or papillate. Medulla K + sordid brown, PD + red (fumarprotocetraric acid aggr.); K+ red, PD ± orange (norstictic and salazinic acids), or K−, PD− (no medullary substances). Antarctic islands, Falkland Is (abnormal form) .... **4. U. aurantiaco-atra** (p. 62)
4b Axis thin, less than half branch diameter. Surface smooth, faveolate or minutely papillate. Medulla K−, PD+ yellow (psoromic acid); or K−, PD− (± fatty acids). Patagonia .... **7. U. neuropogonoides** (p. 80)

5a (2b) Medulla lax, at least towards axis. Axis less than half branch diameter 6
5b Medulla compact. Axis half or more than half branch diameter 7

6a (5a) Apothecia ± lateral, rarely subterminal, subsessile, often in series; mature disc black, marginal excipular rays sparse (10–20) or absent. Surface smooth, waxy, rarely minutely papillate (× 10 lens); rarely with fibrils. Medulla K−, PD− (no medullary substances); or very rarely K−, PD+ yellow (psoromic acid). Patagonia .... **9. U. perpusilla** (p. 85)
6b Apothecia ± subterminal; mature disc rufous brown; marginal excipular rays numerous (20+). Surface ± matt, faveolate to grossly papillate; with numerous fibrils. Medulla K+ red, PD± orange (norstictic and salazinic acids); K−, PD+ yellow (psoromic acid); or K−, PD− (± fatty acids). Kerguelia, Patagonia, Falkland Is..................... **15. U. trachycarpa** (p. 110)

7a (5b) Axis thick, partially sub-divided, often protruding through the cortex as pale maculae. Medulla reduced, penetrating axial cavities. K−, PD− (no medullary substances), very rarely K−, PD+ red (fumarprotocetraric acid). Kerguelia...... **14. U. taylorii** (p. 108)
7b Axis entire, rarely with sinuose outline, not penetrated by the medulla. Medullary chemistry various 8

8a (7b) Surface smooth, subfaveolate, fibrils absent 9
8b Surface papillate or verrucose; often with fibrils 12

9a (8a) Black-edged annulations frequent on main branches. Excipulum smooth with conspicuous marginal rays. Australasia 10

9b Black-edged annulations normally absent. Excipulum faveolate or rarely papillate, marginal rays sparse or absent. Patagonia, Antarctic peninsula and islands 11

10a (9a) Thallus entirely erect. Apothecia subterminal, rarely lateral. Medulla K+ red, PD± orange (norstictic and salazinic acids) .... **5. U. ciliata** (p. 74)

10b Thallus subdecumbent with numerous extended, capillaceous, secondary branches. Apothecia lateral. Medulla K+ red, PD ± orange (norstictic and salazinic acids, ± protocetraric acid); UV ++ blue, K± purple (squamatic, ± hypothamnolic acids); or K−, PD + yellow (psoromic acid) .... **13. U. subcapillaris** (p. 104)

11a (9b) Apothecia lateral, often in series; rarely subterminal, excipulum faveolate. Medulla K−, PD− (no medullary substances); rarely K−, PD + yellow (psoromic acid). Patagonia (abnormal form) .... **9. U. perpusilla** (p. 85)

11b Apothecia subterminal, rarely lateral, excipulum smooth to minutely papillate or verrucose. Medulla K + red, PD ± orange (norstictic and salazinic acids); K + sordid brown, PD + red (fumarprotocetraric acid aggr.); or K−, PD− (no medullary substances). Patagonia, Falkland Is., Antarctic peninsula and islands, including Bouvetøy (abnormal form) .... **4. U. aurantiaco-atra** (p. 62)

12a (8b) Mature apothecial disc rufous brown, marginal excipular rays numerous (20+). Fibrils numerous on main branches. Medulla K + red, PD ± orange (norstictic and salazinic acids); K−, PD + yellow (psoromic acid); or K−, PD− (± fatty acids). Kerguelia, Patagonia, Falkland Is (abnormal form) .... **15. U. trachycarpa** (p. 110)

12b Mature apothecial disc black (rarely brown when immature), marginal excipular rays sparse (10–20) or absent. Fibrils rare on main branches. Medulla K+ red, PD− orange (norstictic and salazinic acids); K+ sordid brown, PD+ red (fumarprotocetraric acid aggr.) or K−, PD− (no medullary substances). Patagonia, Falkland Is., Antarctic peninsula and islands, including Bouvetøy .... **4. U. aurantiaco-atra** (p. 62)

13a (1b) Thallus with true isidia 14

13b Thallus with soredia and/or pseudoisidia 17

14a(13a) Thallus yellow or yellow green; ± pigmented; rarely with fibrils. Pseudocyphellae absent or inconspicuous. Norstictic and salazinic acids absent 15

14b Thallus grey-green, with numerous fibrils. Pigmented isidia arising from prominent pseudocyphellae. Norstictic or salazinic acids usually present. South America .... [**U. amblyoclada** (p. 115)]

15a(14a) Medulla lax throughout. Axis less than half branch diameter. Surface smooth to subpapillate; faveolate to inflated 16

15b Medulla ± compact, rarely sublax. Axis more than half branch diameter. Surface waxy, epapillate, not inflated. Isidia delimited, frequently pigmented and regenerating to form pseudoisidia which may erode. Australasia .... [**U. torulosa** (p. 117)]

16a(15a) Thallus corticolous, rarely saxicolous, ± unpigmented, rarely subpapillate. Isidia scattered, often pigmented. Medulla K−, PD+ yellow, UV− (psoromic acid); K−, PD−, UV++ blue (squamatic acid); rarely K−, PD−, UV− (± fatty acid). Australasia .... [**U. inermis** (p. 117)]

16b Thallus saxicolous, rarely terricolous, often pigmented, subpapillate. Isidia unpigmented, arising from distinct tubercules. Medulla K−, PD− (no medullary substances). Peru, Ecuador, Bolivia (high altitudes) .... **1. U. acanthella** (p. 47)

17a(13a) Medulla lax in main branches. Axis half or less than half branch diameter 18

17b Medulla compact in main branches. Axis more than half branch diameter 23

18a(17a) Main branches extensively inflated or ± articulate 19

18b Main branches only faveolate or slightly expanded 20

19a(18a) Thallus truly sorediate, extensively pigmented or variegated towards apices. Medulla K−, PD− (no medullary substances). Peru, Ecuador, Bolivia. High altitudes (abnormal form) .... **11. U. sphacelata** (p. 92)

19b Thallus pseudoisidiate, pigmentation confined to pseudoisidia, thallus base and branch apices. Medulla K+ red, PD± orange (norstictic and salazinic acids); rarely K−, PD− (no medullary substances). South America .... **6. U. durietzii** (p. 78)

20a(18b) Thallus with fibrils or grossly papillate, arising from a ± proliferating holdfast. Soredia present, pseudoisidia rare. Medulla K+ red, PD± orange (norstictic and salazinic acids); or K−, PD− (no medullary substances). Patagonia, Antarctic peninsula .... **12. U. subantarctica** (p. 99)

20b Thallus smooth to subpapillate (×10 lens), arising from a delimited, or rarely proliferating holdfast. Soredia or pseudoisidia present. Medulla K−, PD− (no medullary substances or ± fatty acids); rarely K−, PD+ yellow (psoromic acid); or K+ red, PD± orange (norstictic and salazinic acids) 21

21a(20b) Soralia delimited, often globose and pigmented. Thallus ± extensively pigmented. Medullary chemistry various 22

21b Soralia eroded, ± effuse to ulcerose, with small blackened pseudoisidia. Thallus pigment confined to base and apices. Medulla K−, PD− (fatty acids). Patagonia, ?South Africa .... **8. U. patagonica** (p. 82)

22a(21a) Medulla containing norstictic acid (K + red, PD ± orange) Patagonia (abnormal form) **12. U. subantarctica** (p. 99)

22b Medulla depsidone deficient (K−, PD−) or rarely containing psoromic acid (K−, PD+ yellow). Bipolar .... **11. U. sphacelata** (p. 92)

23a(17b) Thallus epapillate, waxy, black-edged annulations present or absent 24

23b Thallus papillate, subpapillate or with fibrils; rarely waxy or annulate 26

24a(23a) Thallus bright yellow, torulose, lacking annulations. Pseudoisidia pigmented; regenerating from true isidia. Medullary chemistry various but never containing norstictic and salazinic acids. Australasia .... [**U. torulosa** (p. 117)]

24b Thallus yellow-green (straminous in herbaria), monopodial to richly branched, usually at least with black-edged annulations. Medullary chemistry various, often containing norstictic and salazinic acids 25

25a(24b) Thallus ± subdecumbent, richly branched from a delimited holdfast, with numerous, fragile, capillaceous, divergent ultimate branches. Soralia pale, punctiform. Medulla K+ red, PD± orange (norstictic and salazinic acids). New Zealand .... **10. U. pseudocapillaris** (p. 89)

25b Thallus erect, ± monopodial or moderately branched, often from a proliferating holdfast. Soralia plane, pale, rarely nodular, corticate then pigmented; pseudoisidia rare. Medulla K+ red, PD+ orange (norstictic and salazinic acids); K−, PD− (no medullary substances) (rare); or K−, PD + yellow (psoromic acid) (rare). Australasia, Patagonia; Antarctic peninsula and islands (rare). [If lacking annulations and from Antarctica see also **U. sphacelata** (p. 92) .... **2. U. acromelana** (p. 48)

26a(23b) Thallus ± monopodial or moderately branched arising from a proliferating holdfast; extensively pigmented 27

26b Thallus ± subdichotomously to richly branched arising from a ± delimited holdfast; extent of pigmentation variable 28

27a(26a) Surface ± matt, with fibrils or grossly papillate. Medulla K+ red, PD+ orange (norstictic and salazinic acids), or K− PD− (no medullary substances). Patagonia, Antarctic peninsula .... **12. U. subantarctica** (p. 99)

27b Surface waxy, subpapillate. Medulla K−, PD−, (no medullary substances). Antarctica (abnormal form) .... **11. U. sphacelata** (p. 92)

28a(26b) Soralia plane, crateriform; minute pseudoisidia rare. Thallus grossly papillate; usually matt; annulations absent. Medulla compact; K−, PD− (no medullary substances); or K+ sordid brown, PD + red (fumarprotocetraric acid); rarely K+ red, PD ± orange (norstictic and salazinic acids – Falkland Is.). Antarctic continent, subantarctic islands, New Zealand (rare), Patagonia (rare) .... **3. U. antarctica** (p. 55)

28b Soralia plane, eroded, ulcerose; minute pigmented pseudoisidia frequent. Thallus smooth, waxy to subpapillate; occasionally annulate. Medulla sometimes lax in part; K−, PD− (fatty acids) Patagonia, ? South Africa .... **8. U. patagonica** (p. 82)

The species

1. **Usnea acanthella** (Lamb) F. J. Walker, **comb. nov.** **Fig. 9**

Neuropogon sulphureus f. *acanthella* Lamb in *J. Linn. Soc.* (Bot.) **52**: 210 (1939). Type: Peru, [Puno], Carabaya, above Limbani, 4410 m, 18 November 1937, *Dora Stafford* 1108 (BM! – holotype; BM!, FH! – isotypes). [TLC: no medullary substances, ± traces of unidentified fatty acids, usnic acid.]

Description: Thallus 2–4 cm, arising from a delimited, blackened, ± elongated, stalked holdfast, erect or rarely ± subdecumbent, ± subdichotomous to richly, ± divergently branched above, without fibrils, with loosely interwoven, capillaceous, spinulose secondary branches. Branches terete, greenish yellow, with ± broad bands of black pigment, inflated, ± weakly articulated. Cortex thin. Surface ± faveolate, matt, subpapillate. Medulla extremely lax, axis thin, occupying 0·2–0·3 of the branch diameter. Isidia present, fine, spinulose, unpigmented, *c.* 0·5 mm long, frequently eroding, arising in delimited clusters from partially corticate tubercules. Pseudoisidia and soredia absent. Apothecia and pycnidia not seen. TLC: no medullary substances, ± traces of unidentified fatty acids, usnic acid.

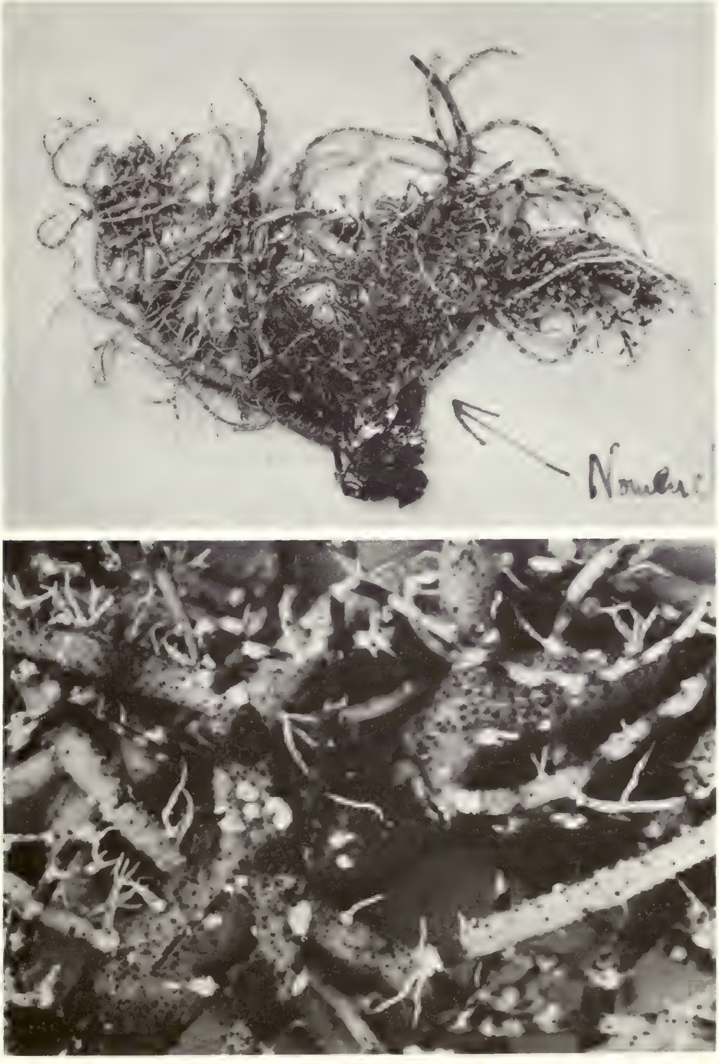


Fig. 9 *Usnea acanthella.* Holotype of *Usnea suiphurea* f. *acanthella* Lamb (BM). Top. Whole thallus (×1·5). Bottom. Detail of isidia (×10).

Distinguishing features: *Usnea acanthella* is characterised by its erect, spreading habit from a basal stalk and a richly branched, spinulose thallus, an inflated, subpapillate surface, a lax medulla lacking depsides and depsidones, a thin axis, and clusters of fine, unpigmented, true isidia.

Distribution: *Usnea acanthella* is apparently restricted to saxicolous, or rarely musicolous-terricolous habitats, in open páramo at high altitudes in the northern part of the Andean chain. The species has been recorded from between 3500–4500 m in Peru, Ecuador, and Bolivia. Fig. 7.

Chemistry: Only known in a depsidone deficient phase, with the occasional occurrence of traces of unidentified fatty acids.

Variation: From the small number of collections studied, *Usnea acanthella* appears to be a constant species with little variation. The isidia often erode or appear nodular, but even when they are abraded or underdeveloped, the thallus is characterised by the prominent, pale tubercules from which they arise. Occasionally small fibrils may develop secondarily from such tubercules. There is some variation in the habit of the species, ranging from thalli with prominent, inflated main branches and relatively few ultimate branches, to richly branched, less inflated forms with extensively interwoven branches.

Although the type material is uniform in its variegation, frequently with broad bands of pigmentation, other gatherings indicate that this may not necessarily be as constant a feature of this species. In recent collections from Ecuador some parts of the thalli are unpigmented, whilst other areas are totally blackened. Such presence or absence is reminiscent of the kind of blackening found in some corticolous species belonging to the subgenus *Usnea*, for example *U. inermis* (p. 117), where blackening only occurs in extremely exposed situations or when the thallus is moribund. However, the presence of some distinctly variegated thalli indicates that pigmentation is probably the norm for the species, although a wider range of material is required to verify its extent.

Species concept: Lamb (1939*a*) described this taxon as a form of *Usnea sphacelata* (as *U. sulphurea*), interpreting the pale isidia as outgrowths from healed-over soralia rather than recognising their true nature. The development of true isidia in this species widens the range of asexual propagules found in the subgenus and their development is a sufficiently distinct feature, combined with the characteristic habit of the thallus, to warrant separation at species level.

The species superficially is very similar to *Usnea durietzii* and *U. sphacelata*, sharing the common features of a lax medulla and normally saxicolous habitat. The development of a basal stalk below and branching are very reminiscent of *U. durietzii*, although the branches in *U. acanthella* are generally finer and more fragile. *U. acanthella* may be distinguished from all other asexual species of the subgenus by the presence of true isidia.

Specimens examined

ECUADOR. Chimborazo: Cerro Payacorral, near El Altar, 3450 m, 2 August 1980, *Cambridge Exped.* 2 (BM); Mt. Achipungo, near Osogochi, 4500 m, 7 September 1980, *Cambridge Exped.* 42 (BM); near El Altar, near Riobamba, 4150 m, 3 August 1980, *Cambridge Exped.* 5 p.p. (BM).

PERU. Cuzco: Huaya Pass, above Cuzco, 4500 m, 14 June 1973, *B. Mullins* 29 (BM). Puno: prope Azangaro, June 1854, *W. Lechler Pl. Peruvianae* 1758 p.p. (BM); Cordillera de Carabaya, Limbani (type locality).

BOLIVIA. La Paz: Larecaja, Sorata, 4500 m, April 1897, *G. Mandon* 1737 p.p. (PC).

2. **Usnea acromelana** Stirton **Figs 10–12**

in *Trans. Proc. N.Z. Inst.* **30**: 388 (1898). – *Neuropogon acromelanus* (Stirton) Lamb in *J. Linn. Soc.* (Bot.) **52**: 218 (1939). Type: New Zealand, Selwyn Gorge, May 1894, *T. W. N. Beckett* L11, 'on trees' (thalli saxicolous) (BM! – holotype; CANL 16943!, CHR 343153! – isotypes; GLAM NHB 1927-8-562! – ? isotype). [TLC: norstictic acid, salazinic acid, usnic acid.]

Neuropogon acromelanus var. *decipiens* Lamb in *J. Linn. Soc.* (Bot.) **52**: 219 (1939). – *Usnea acromelana* var. *decipiens* (Lamb) Lamb in *Br. Antarct. Surv. Sci. Rep.* **38**: 5 (1964). Type: Tasmania, summit of Table Mountain [= Mt. Wellington (Wilson, 1893)], *R. Brown Iter Australiense, 1802–05,* 523 (BM! – holotype; BM! – isotype). [TLC: norstictic acid, salazinic acid, usnic acid.]

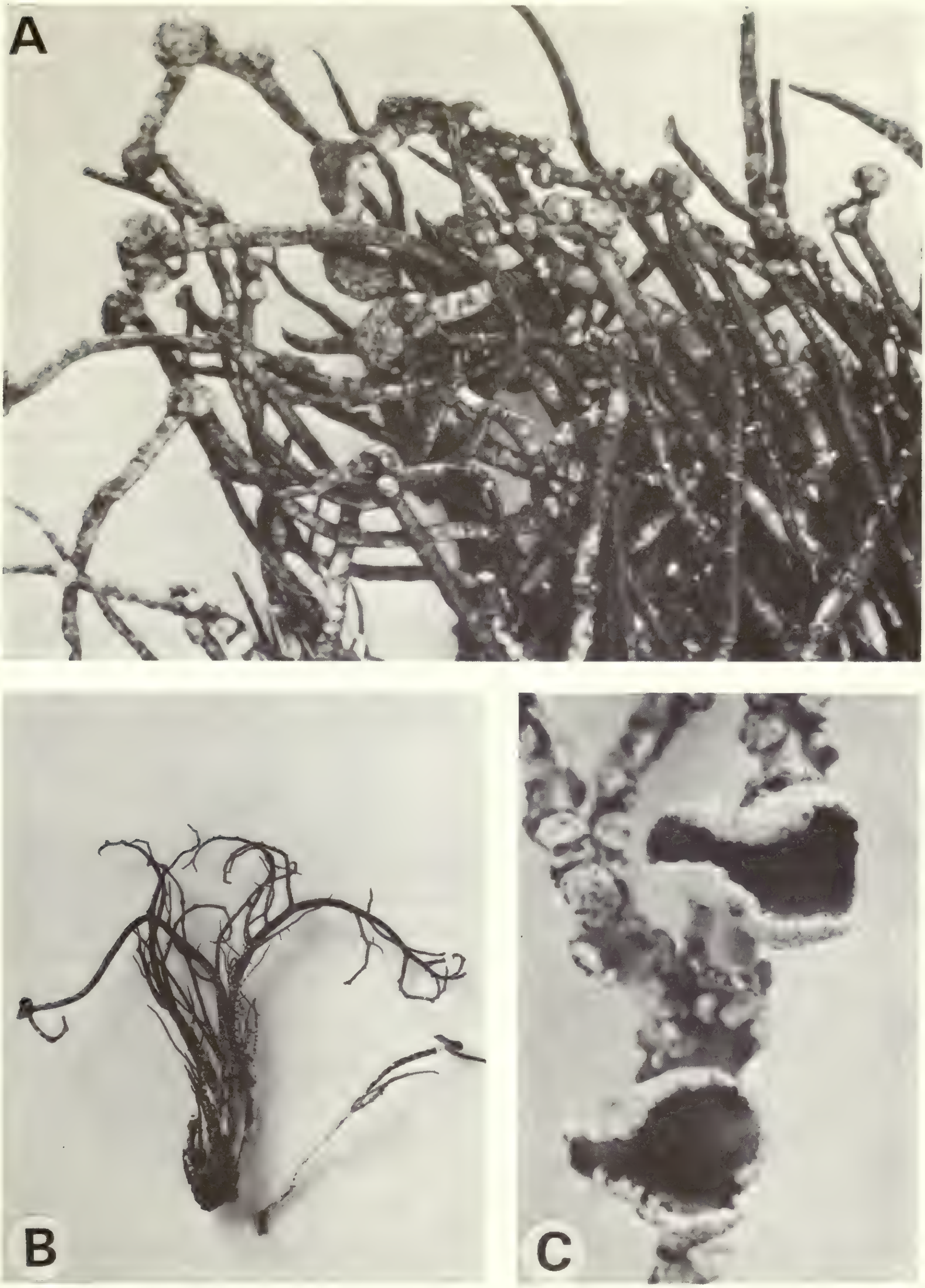


Fig. 10 *Usnea acromelana*. A Convex-globose soralia ×10 (holotype of *Neuropogon acromelanus* var. *decipiens* Lamb, BM). B, C Fertile thalli. B Antarctic peninsula, Joinville I., *Smith* 2680 (AAS) ×1·5. C New Zealand, Otago, Old Man Range, *James* 1597 (BM) ×10.

Description: Thallus (1·5–2–4(–6) cm, arising from a broadly proliferating or rarely delimited, pigmented holdfast, usually erect, ± monopodial or subdichotomous, moderately branched above, usually lacking fibrils. Branches terete, yellow-green, ± continuously pigmented violaceous black towards the apices. Cortex thick. Surface smooth or rarely subfaveolate, waxy, epapillate, with conspicuous black-edged annulations on main branches. Medulla compact, axis thick, occupying *c.* 0·5 of the branch diameter. Soralia numerous on primary and secondary branches, plane and discrete, sometimes becoming confluent, rarely convex-globose and pulverulent. Soredia granular, unpigmented, or partially corticate then pigmented. Pseudoisidia rare, isidia absent. Apothecia rare, subterminal, as in *U. ciliata*. Pycnidia not seen. TLC: (1) norstictic acid, salazinic acid, ± protocetraric acid, usnic acid; (2) psoromic acid, ± 2′-O-demethylpsoromic acid, usnic acid; (3) no medullary substances, usnic acid.

Distinguishing features: *Usnea acromelana* is characterised by its erect, proliferating habit, and a monopodial to moderately branched thallus, often with violaceous black pigmentation, a smooth, waxy, black-annulate surface, a compact medulla usually containing norstictic and salazinic acids, a thick axis, and numerous emarginate soralia.

Distribution: In Australasia *Usnea acromelana* occurs in the alpine regions of New Zealand and is mainly confined to the Southern Alps apart from isolated records from the North Island, Stewart Island, and Chatham Island; it is rather rare in Tasmania and is known only from a single locality in Victoria. The species is rarely found below *c.* 400 m, usually occurring between 900–1800 m, and is rare at higher altitudes, *c.* 2500 m, occasionally being replaced by *U. sphacelata*.

Usnea acromelana is probably less frequent in southern South America (Patagonia) and the Antarctic peninsula than previously indicated (e.g. Follmann, 1965*a*; Lamb, 1948*a*). For example, specimens from central Chile are referable to *U. patagonica*, although the northern limit of *U. acromelana* is still uncertain. Lamb (1939*a*) reported a single gathering of *U. acromelana* from Peru. This was based on a mixed collection (BM!) of *U. acanthella* and a norstictic acid-containing thallus that appears to be *U. durietzii*. However, Dennis (1960) reported affinities between the fungus flora of South America and Australasia, finding the same species in Tasmania and in the páramos of western Venezuela. Consequently the possible occurrence of *U. acromelana* in the Andes north of Patagonia cannot be completely dismissed.

Usnea acromelana is rare on the Antarctic peninsula and is probably confined to the northern tip and the western coast, where material has been examined from Adelaide, Brabant, Joinville and Wiencke Islands, frequently mixed in gatherings with *Usnea antarctica, U. aurantiaco-atra,* and *U. subantarctica*. The species is also tentatively identified from a few depauperate specimens from the South Orkney Islands, where *U. antarctica* is the dominant species. The species is not known from continental Antarctica and previous reports (Filson, 1975; Rudolph, 1963, 1966) refer to *U. sphacelata*, including the infraspecific taxa described by Lamb (1939*a*). Fig. 6.

Chemistry: Thalli containing norstictic acid and salazinic acid (Race 1) are by far the most frequent of the three chemical races recorded. In this race a trace amount of protocetraric acid is often present, but probably not always in sufficient quantity to enable detection by TLC. This is the most frequent race found in Australasia and is also the most widespread in the South American sector, being previously reported from Patagonia by Asahina (1967), and extends south to the Antarctic peninsula.

The occurrence of psoromic acid (Race 2) is rare and unpredictable, and is known from isolated locations in Argentina and Chile, the former collection also including depsidone deficient thalli (Race 3).

It is possible that there is a correlation between medullary substances and distribution, as Race 3 is chiefly confined to more southern latitudes; the only exception being the isolated record from Victoria, Australia. A parallel case occurs in *Usnea antarctica* where depsidone-containing thalli are only frequent towards the northern part of the distribution of that species.

Variation: The above description is characteristic of the majority of specimens examined and is typical of much New Zealand material and, to a lesser extent, Tasmanian and South American-antarctic populations where a greater range of thallus morphology is often encountered. The greatest range of variation is found in branching, extent of pigmentation and form of the soralia. The extent of branching ranges from monopodial, with numerous primary branches arising from a proliferating holdfast, to richly branched, rarely from a solitary point of attachment.

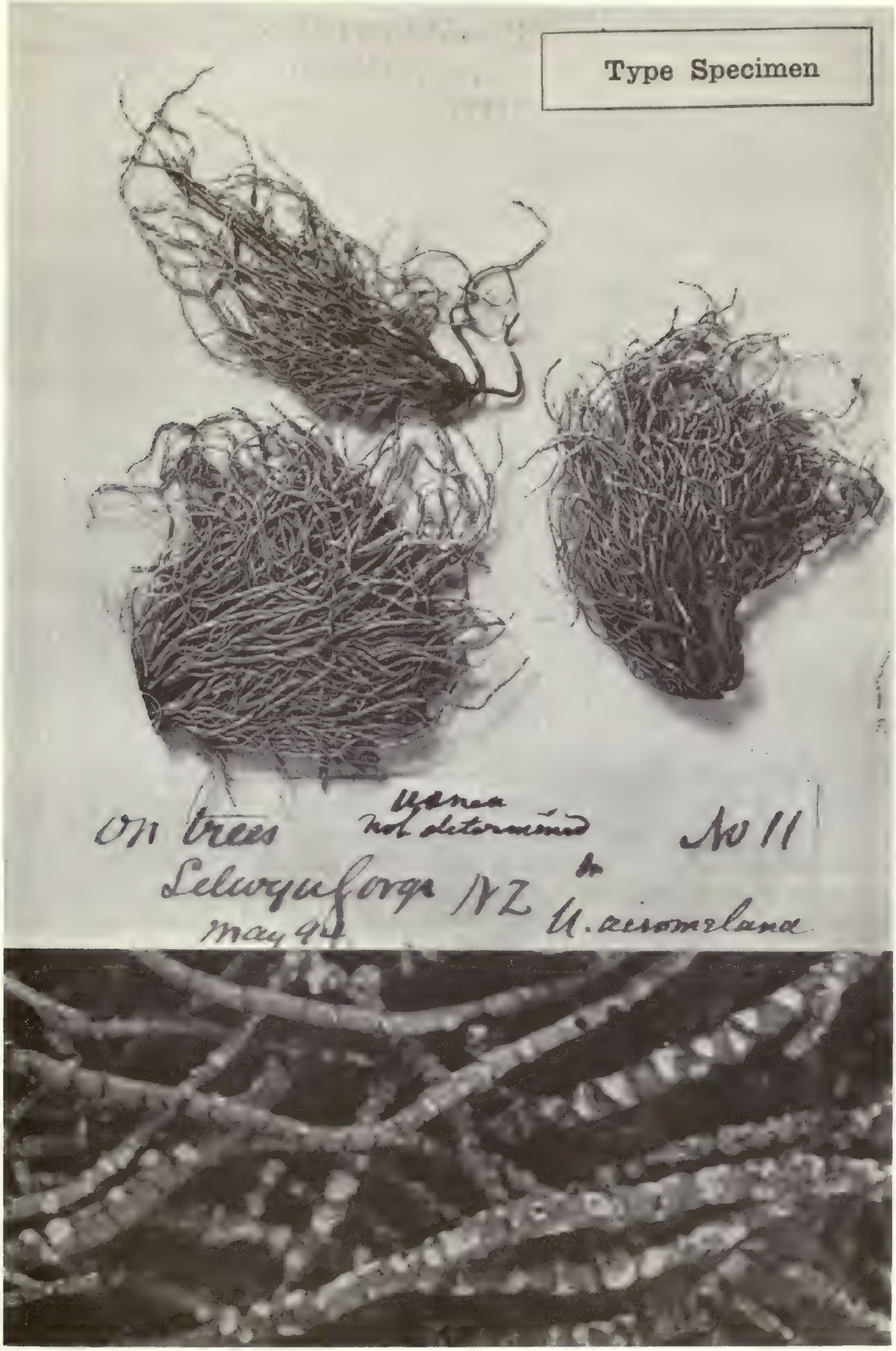

Type Specimen
On trees
Usnea
not determined
No 11
Selwyn Gorge NZ
May 9
to
U. acromelana

Fig. 11 Holotype of *Usnea acromelana* Stirton (BM). Top. ×1. Bottom. Detail of cortical annulations and plane soralia ×10.

Study of a large number of collections, particularly from NewZealand (CHR), indicates that altitude may influence thallus morphology, since less characteristic thalli often occur at lower altitudes. For example, the type material of *Usnea acromelana*, from *c.* 600 m, includes two of the extreme forms encountered. Plants forming the holotype (BM) (Fig. 11) and one isotype (CANL) are infrequently branched, with only traces of pigmentation at the apices, lacking the waxy, violaceous black lustre, having inconspicuous annulations, and large (0·4–0·5 mm), plane soralia that are rarely pigmented-corticate. In contrast, isotype material in CHR (Fig. 12) is less robust, more richly branched, with scattered fibrils, fine, attenuate, pigmented secondary branches, prominent black-edged annulations, smaller (0·1–0·3 mm), unpigmented soralia, and a less densely interwoven medulla.

Scantily pigmented forms are rare at higher altitudes where thalli tend to be smaller, more richly branched and more extensively pigmented, possibly as a response to greater exposure. In extreme instances extensive cracking, resulting from marked annulation formation, may give a slightly faveolate appearance.

In typical specimens the soralia are pale, plane, or slightly excavate, sometimes with a tendency to become convex or slightly confluent, characteristically with a small amount of blackening inside resulting from overlying cortical fragments which, in very extreme instances, may form minute pseudoisidia, or, when damaged, produce spinules. Less typically, soralia may be small and plane, resembling those of *Usnea pseudocapillaris*, or can be large, extensively blackened, convex and globular to nodulose, (Fig. 10) as in the variety *decipiens* (Lamb, 1939*a*). A range of soralia forms may be found on a single thallus.

There appears to be a much wider range of variation in Tasmanian populations of *Usnea acromelana* than in New Zealand, particularly in soralia type and branching pattern; some specimens may lack annulations. Such unusual forms are occasionally found in other parts of the range of this species. In Tasmanian material two main types may be distinguished, but neither is here considered worthy of taxonomic status. The first conforms to variety *decipiens* and is small (2–4 cm), erect, richly branched, extensively pigmented, with large (0·5–1·5 mm), nodular, blackened soralia with compacted soredia. The second type is erect to subdecumbent, more divergently branched, and could be regarded as an intermediate between *U. acromelana* and *U. pseudocapillaris*. However this is considered to be a form of *U. acromelana* as secondary branches are notably coarser than those of *U. pseudocapillaris*. Ultimate branches are shortly attenuate and capillaceous, giving the thallus a slightly tasselled and interwoven appearance; the soralia are small, plane to punctiform, rarely pigmented, and confined to secondary branches. The thalli lack the segmented appearance, the extended, entangled secondary branches, and laxer medulla, characters which distinguish *U. pseudocapillaris*.

In some respects South American and antarctic populations of *Usnea acromelana* appear to be slightly different from those in Australasia. Thalli may frequently be more robust or more richly branched; short incipient fibrils are rare and are unrelated to papillae. In addition such thalli are usually extensively pigmented, including some banded or mottled variegation which is not generally a feature of this species. As in Australasian populations the extent of black-edged annulations is variable. Often folding and puckering of the surface may be more pronounced, becoming faveolate-ridged rather than simply annulate, which might lead to misidentification. Thalli still retain a violaceous tinge to the pigmentation and a waxy lustre, whilst soralia exhibit the same range of forms encountered in Tasmanian populations.

Apothecia are rarely produced (Fig. 10) and are only known from a few localities, for example, from the Old Man Range, Otago, New Zealand (*P. W. James* 1597, BM!) and Joinville Island, Antarctic peninsula (*R. I. L. Smith* 3680 p.p., AAS!). The New Zealand specimens bear subterminal or rarely lateral apothecia with a rayed excipulum, which frequently bear soralia, and a buff-grey to greenish black disc. Although sometimes lacking pigment, the disc colour is distinct from that of *Usnea trachycarpa* which is rufous brown. The Antarctic peninsula specimen belongs to Race 1 and bears a single apothecium, *c.* 2 mm diameter, with a black disc but lacks excipular rays. Lamb (1948*a*) described a fertile specimen of this species from Wiencke Island, Antarctic peninsula. This has been examined (*Lamb* 1790 p.p. BM!) and is similar to the Joinville Island specimen.

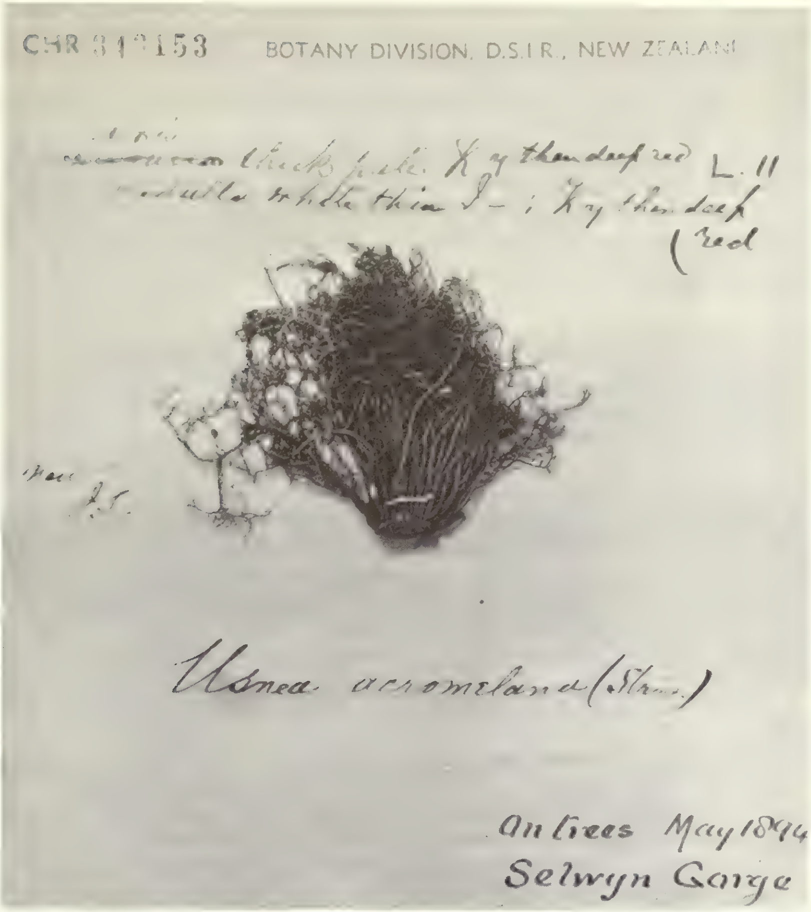

BOTANY DIVISION, D.S.I.R., NEW ZEALAN
L. 11
Usnea acromelana (Stirt.)
On trees May 1894
Selwyn Gorge

Fig. 12 Isotype of *Usnea acromelana* Stirton (CHR) ×1.

Species concept: The diverse range of forms of *Usnea acromelana* that occur might appear to be distinct taxa if it were not for the existence of a range of intermediates. Initially, study of the varied type material of *U. acromelana* caused considerable speculation as to the delimitation of this species, however, these extremes are here considered to fall within the variation of a single species. This is particularly true of Tasmanian populations, and it is possible that the species is diverging into a range of entities, some of which already differ from New Zealand populations. Some of these forms may appear quite distinct when observed individually but *en masse* form a continuum.

The diversity of chemical races in South American populations may indicate possible affinities with other species occurring in that sector. Such specimens are here referred to *Usnea acromelana*, despite some morphological ambiguities which are not sufficient to warrant recognition of separate taxa. Further collections and ecological data are essential to resolve this problem.

Usnea acromelana is most closely related to *U. pseudocapillaris* and both belong to the *U. ciliata* complex. As frequently occurs within the subgenus, there are a few specific instances where it is difficult to conclusively separate the two species. However, study of populations indicates that there are sufficient distinguishing and constant characters. *U. pseudocapillaris* can normally easily be identified (p. 90) on morphological and chemical characters.

On rare occasions in Australasia *Usnea acromelana* may be confused with *Usnea torulosa*

(Appendix I, p. 117). The two species may be separated by the twisted, entwined habit of *U. torulosa*, its brighter yellow colouration in the field (although this may be less obvious in stored material), lack of surface pigmentation, the presence of pigmented, true isidia, and by differences in depsidone content. The type of *Neuropogon acromelanus* var. *inactivus* (Lamb, 1939*a*) from Tasmania is *U. torulosa.*

Usnea acromelana can be distinguished from *U. antarctica* by the waxy surface and absence of papillae, and margin to the soralia; from *U. durietzii* and *U. patagonica* by differences in habit and absence of pseudoisidia; and from *U. sphacelata* and *U. subantarctica* by a compact medulla and smooth surface.

Selected specimens examined
Race 1
CHILE. Magallanes: Seno Skyring, Estancia Maria, near sea-shore, 28 April 1940, *R. Santesson* 7058 (S, UPS); Tierra del Fuego, [54°32′S: 70°04′W], 730 m, 24 February 1978, *J. R. Peart* s.n. (BM); Tierra del Fuego, Sierra Sorondo, N. slope, above Las Cotorras (*c.* 20 km ENE. of Ushuaia), 800 m, 6 February 1940, *R. Santesson* 641d (S); Tierre del Fuego, Sierra Alvear, S. slope, above Las Cotorras (*c.* 20 km ENE. of Ushuaia), 700 m, 9 February 1940, *R. Santesson* 637d (S); Isla Navarino, Puerto Navarino, 10 m, 28 February 1940, *R. Santesson* 1232b (S); Canal Beagle, Yendegaia, by front of glacier, 50–100 m, 4 March 1940, *R. Santesson* 1373 (S), 1373 p.p. (UPS).
ARGENTINA. Santa Cruz: Lago Argentino, near front of Ventrisquero Mayo, 105 m, March 1959, *P. W. James* 5053 (BM); Lago Argentino, Cerro Mayo, *c.* 1500 m, 25 February 1959, *P. W. James* 3605 (BM, S, UPS, US); Lago Argentino, Peninsula Magallanes, opposite Spegazzini Glacier, Ventrisquero Spegazzini, January 1959, *P. W. James* s.n. (BM); Calafate, 1959, *P. W. James* s.n. (BM); Lago San Martin, 1600 m, 2 February 1933, *A. Donat* 3 p.p. (H). Tierra del Fuego: Parque Nacional Tierra del Fuego, Ushuaia, 'Weg zum' Glaciar Martial, *c.* 500 m, 7 December 1973, *A. Henssen & G. Vobis* 24417i p.p. (MB).
SOUTH ORKNEY IS. Coronation I.: Wave Peak Buttress, 225 m, 9 September 1973, *T. N. Hooker* 84 (AAS), *T. N. Hooker* 87 (AAS), *T. N. Hooker* 116 (AAS); Sunshine Glacier, 180 m, 12 March 1972, *T. N. Hooker* 66 (AAS).
ANTARCTIC PENINSULA. Graham Land: Joinville I. [63°15′S: 55°45′W], Mt. Alexander, 200–500 m, 27 March 1981, *R. I. L. Smith* 2680 p.p. (fertile) (AAS); Mt. Cardinall [63°27′S: 57°10′W], 225 m, 14 December 1946, *J. D. Andrew* F.I.D.S. D115-12b (BM); Gerlache Channel, Brabant I. [64°15′S: 62°20′W], *Exped. Antarct. Belge* 249 p.p. (BM ex herb. Vainio 354, 355); Palmer Archipelago, Wiencke I. [64°48′S: 63°25′W], N. buttress of Noble Peak, 225 m, 20 November 1944, *I. M. Lamb* 1790 p.p. (fertile) (BM); Loubet Coast, Adelaide I., Rothera Point [67°35′S: 68°00′W], 10 m, 29 January 1976, *J. Fenton* 23 (AAS).
AUSTRALIA. Tasmania: Central Southern Tasmania, Mt. Mawson, 1220 m, 4 December 1965, *G. C. Bratt* 2931a (CHR 343400); Mt. Mawson, southern peak, 1220 m, 11 May 1968, *G. C. Bratt* 68/348 [Lich. Exs. COLO 247] (BM, CHR 343460); Mt. Mawson, 19 February 1968, *R. Filson* 10580 (MEL 1029344); Lake Augusta, outcrop *c.* 0·5 km E. of dam, 840 m, 2 March 1970, *G. C. Bratt & M. H. Bratt* Bratt 70/243 (HO 35238), Bratt 70/229 (HO 35237); Mt. Wellington Plateau, 11 January 1969, *G. C. Bratt* et al. Bratt 69/7 (HO 35193), summit area, 1270 m, 20 December 1964, *G. C. Bratt* 1872b (HO 35188), 1850, *S. Mossman* 796 (BM, E); Table Mtn, 1095 m, 18 June 1972, *G. C. Bratt & J. A. Cashin* Bratt 72/393 p.p. (HO 35179); Mt. Penny, 4 April 1969, *G. C. Bratt & K. M. Mackay* Bratt 69/162a&b (HO 35240).
NEW ZEALAND. North Island. Wellington: Tongariro National Park, Tama Lakes, 1220 m, *D. Scott* 504 (OTA): unlocalised: *Colenso* C1776 (BM, WELT). South Island. Nelson: Cobb Valley, Cobb Ridge, 850 m, 19 December 1982, *J. K. Bartlett* 26252 (herb. Bartlett, BM); Mt. Technical, above Lewis Pass, 14 January 1979, *D. J. Galloway* s.n. (CHR 343160 p.p.); Mt. Arthur, March 1879, *A. Mckay* s.n. (WELT L1505). Marlborough: Inland Kaikoura Range, Mt. Tapuaenuku, 20 March 1934, *J. S. Thomson* 1523 p.p. (CHR 343806 p.p.), 2400 m, *J. S. Thomson* 1506 p.p. (CHR 343791 p.p.); Branch River, Range above Gordon Stream, *c.* 900–1200 m, 23 January 1984, *J. K. Bartlett* 26418b p.p. (herb. Bartlett), 26419 p.p. (herb. Bartlett). Canterbury: Banks Peninsula, Mt. Sinclair, 3 February 1979, *D. J. Galloway* s.n. (CHR 343147); Ben Ohau Range, Glen Lyon Station, 1830 m, October 1958, *J. Murray* Mason 29 & 30 (BM, OTA, S, UPS); Kirkliston Range, 1520–1680 m, 25 March 1978, *D. J. Galloway* s.n. (CHR 343230); Four Peaks Range, Blue Mtn, *c.* 1640 m, 23 April 1979, *D. J. Galloway* s.n. (CHR 343224); Torlesse Range, Foggy Peak, 1680 m, November 1972, *D. J. Galloway* s.n. (CHR 343430). Otago: Humboldt Mtns, Mt. Minos, 2010 m, 1 January 1970, *D. J. Galloway* s.n. (CHR 342824); Rock and Pillar Range, 1160–1190 m, 18 September 1981, *F. J. Walker* s.n. (BM, UPS); Dunedin, Maungatua, 880 m, 17 September 1981, *F. J. Walker* s.n. (BM, UPS); Dunedin, Middlemarch–Mosgiel road, nr. Sutton, *c.* 370 m, 18 September 1981, *F. J. Walker* s.n. (BM); Old Man Range, 1220 m, 1 February 1963, *P. W. James* 1597 (BM), 1579 (BM);

Matukituki Valley, Mt. Avalanche, 2560–2590 m, 15 February 1969, *L. D. Kennedy* s.n. (CHR 343382), Mt. Sir William, 2560 m, 27 December 1970, *D. J. Galloway* s.n. (CHR 342786 p.p.); Shepherd's Pass, 1980 m, January 1968, *D. J. Galloway* s.n. (fertile) (CHR 343411); Mt. Earnslaw, 2700 m, February 1972, *A. A. Deans* s.n. (CHR 342757); Remarkables, above Lake Alta, 1980 m, March 1967, *L. D. Kennedy* s.n. (fertile) (CHR 343440). Southland: Mid Dome, 1520 m, May 1970, *G. Van Reenen* s.n. p.p. (CHR 342837 p.p.); Mt. Barrier, Homer Tunnel, March 1959, *M. A. Chapman* Murray 4180 (OTA). Stewart I.: Mt. Anglem, summit, 984 m, February 1966, *D. J. Galloway* s.n. (CHR 343356, CHR 343417, CHR 343389). Chatham Is: Chatham I., *Travers* s.n. (BM).

Race 2

CHILE. Aisén: 'in valle superiore fluminis Aysén', *c.* 1400 m, 23 February 1897, *P. Dusén* s.n. (UPS).

ARGENTINA. Santa Cruz: Lago Argentino, Cerro Norte, *c.* 800 m, 22 December 1958, *P. W. James* 404 p.p. (BM).

Race 3

CHILE. Magallanes: Tierra del Fuego, Isla Navarino, 300 m, 1963, *G. Follmann* 14586 p.p. (M).

ARGENTINA. Santa Cruz: Lago Argentino, Glaciar Moreno, 22 January 1967, *P. R. San Martin* s.n. (FH); Lago Argentino, Parque Nacional Glaciares, Peninsula Magallanes, 17 December 1973, *A. Henssen & G. Vobis* 24516a (MB); opposite Spegazzini Glacier, *P. W. James* s.n. p.p. [as Race 1] (BM); Lago Argentino, Bilbao, 2–3 February 1914, *C. M. Hicken* 16450 (BM); Cerro Norte, *P. W. James* s.n. p.p. [as Race 2] (BM). Unlocalised: South Patagonia, 1900–01, comm. H. Prichard (BM).

SOUTH ORKNEY IS: Coronation I., Wave Peak Buttress, 225 m, 9 September 1973, *T. N. Hooker* 85 (AAS), *T. N. Hooker* 86 (AAS), *T. N. Hooker* 115 (AAS), *T. N. Hooker* 117 (AAS), *T. N. Hooker* 118 (AAS).

AUSTRALIA. Victoria: Basalt Hill, Bogong High Plains, [*c.* 2000 m], 29 January 1967, *A. C. Beauglehole* s.n. (MEL 18755), 22 January 1967, *R. B. Filson* 9504 (MEL 1018193).

For further localities of Race 1 in Canterbury and Otago see lists held in BM and collections in BM, CHR, HO and OTA.

3. **Usnea antarctica** Du Rietz **Figs 13–14**

in *Svensk bot. Tidskr.* **20**: 93 (1926). – *Neuropogon antarcticus* (Du Rietz) Lamb in *J. Linn. Soc.* (Bot.) **52**: 210 (1939). Type: Regio Antarctica, South Victoria Land, Admiralty Range, 2000′ s.m., 1900, *C. R. Borchgrevink* (UPS! – holotype; S!, O! – isotypes). [TLC: no medullary substances; ± UV+ unknowns, usnic acid.]

Neuropogon melaxanthus f. *sorediifer* Crombie in *J. Linn. Soc.* (Bot.) **15**: 182 (1876). – *Usnea melaxantha* var. *sorediifera* (Crombie) Müll. Arg. in *J. Linn. Soc.* (Bot.) **32**: 200 (1896). – *Usnea sulphurea* var. *sorediifera* (Crombie) Vainio, *Rés. Voy. S. Y. Belgica, 1897–99, Botan., Lichens*: 11 (1903). – *Neuropogon antarcticus* f. *sorediifer* (Crombie) Lamb in *J. Linn. Soc.* (Bot.) **52**: 213 (1939). Type: Kerguelen Land, Royal Sound, Venus Transit Expedition, *A. E. Eaton* (BM! – lectotype, selected Lamb, 1939*a*; BM!, M!, UPS! – isolectotypes). [TLC: fumarprotocetraric acid aggr., usnic acid.]

Usnea sulphurea var. *granulifera* Vainio, *Rés. Voy. S. Y. Belgica, 1897–99, Botan., Lichens*: 11 (1903). – *Usnea melaxantha* var. *granulifera* (Vainio) Hue, *Deux Exped. Antarct. Franç. Lichenes*: 27 (1915). – *Usnea granulifera* (Vainio) Motyka, *Lich. Gen. Usn. Stud. Monogr.* **1**: 35 (1936). Type: Détroit de Gerlache: dans les fentes d'une falaise rocheuse, Cap Anna Osterrieth, 64°33′ de latitude sud, Terre de Danco (9e débarquement, 197 p.p.), *M. Émile G. Racovitza* (TUR 443 herb. Vainio 358! – lectotype, selected Dodge, 1973; herb. Dodge – isolectotype, not seen). [TLC: no medullary substances, usnic acid.] (see Note 1)

Neuropogon insularis Lamb in *J. Linn. Soc.* (Bot.) **52**: 215 (1939). – *Usnea insularis* (Lamb) Dodge in *Rep. B.A.N.Z. Antarctic Res. Exp.* B, **7**: 211 (1948). Type: Prince Edward Group: Marion I., 26 December 1873, *Challenger Exped.* (BM! – holotype; BM! – isotype). [TLC: fumarprotocetraric acid aggr., usnic acid.]

Usnea crombiei ['*Crombii*'] Dodge in *Rep. B.A.N.Z. Antarctic Res. Exp.* B, **7**: 212 (1948); nom. inval. (Article 36.1.). Spec. orig.: Heard I., between Atlas Cove and Corinthian Bay, *B.A.N.Z.A.R.E.* B140–36 (herb. Dodge, not seen). [TLC: fumarprotocetraric acid, usnic acid (Lamb, 1964) AD! – loc. classicus.]

Usnea crombiei var. *sublaevis* Dodge in *Rep. B.A.N.Z. Antarctic Res. Exp.* B, **7**: 213 (1948); nom. inval. (Article 36.1) Spec. orig.: Heard I., between Atlas Cove and Corinthian Bay, *B.A.N.Z.A.R.E.* B 140-40 (herb. Dodge, not seen). [TLC: fumarprotocetraric acid, usnic acid (AD! – loc. classicus).]

Usnea floriformis Dodge in *Rep. B.A.N.Z. Antarctic Res. Exp.* B, **7**: 214 (1948). Type: Heard I., Atlas

Cove and Corinthian Bay, *B.A.N.Z.A.R.E.* B 140-41 (herb. Dodge – holotype, not seen). [TLC: fumarprotocetraric acid, usnic acid (AD! – loc. classicus).]

Usnea propagulifera Dodge in *Rep. B.A.N.Z. Antarctic Res. Exp.* B, **7**: 213 (1948). Type: Heard I., Atlas Cove to Corinthian Bay, *B.A.N.Z.A.R.E.* B150-42 (herb. Dodge – holotype, not seen). [TLC: fumarprotocetraric acid aggr., usnic acid (AD! – loc. classicus).]

Usnea pustulata Dodge in *Rep. B.A.N.Z. Antarctic Res. Exp.* B, **7**: 203 (1948). Type: Queen Mary Land, Possession Nunatak [66°45′S: 98°30′E], *C. T. Harrisson* A.A.E. 85-1 (herb. Dodge – holotype, not seen). [TLC: no medullary substances, (Lamb, 1948*a*).]

?*Usnea subfoveolata* Dodge in *Rep. B.A.N.Z. Antarctic Res. Exp.* B, **7**: 202 (1948). Type: Queen Mary Land, Hippo Nunatak [66°26′S: 98°06′E], *C. T. Harrisson* A.A.E. 82-2 (herb. Dodge – holotype, not seen). [Chemistry: no medullary substances (Lamb, unpublished notes, AAS!)] AD! – loc. classicus = *U. sphacelata*. (see Note 2)

?*Usnea subpapillata* Dodge in *Rep. B.A.N.Z. Antarctic Res. Exp.* B, **7**: 204 (1948). Type: Queen Mary Land, Hippo Nunatak, *C. T. Harrisson* A.A.E. 82-3 (herb. Dodge – holotype, not seen). [Chemistry: no medullary substances (Lamb, unpublished notes, AAS!).] AD! – loc. classicus = *U. sphacelata*.

Usnea crassa Zammuto *in* Dodge in *Trans. Am. microsc. Soc.* **84**: 521 (1965). Type: Antarctica, Melchior Is., Eta (Bailey) I. [64°19′S: 62°55′W], 5 March 1941, *P. A. Siple* 349 (herb. Dodge – holotype, not seen; US! – isotype). [TLC: no medullary substances, usnic acid (isotype).]

Usnea pseudofruticosa Zammuto *in* Dodge in *Trans. Am. microsc. Soc.* **84**: 521 (1965). Type: Antarctica, Melchior Is., Gordon Lien I., 7 March 1941, *P. A. Siple* 352 (herb. Dodge – holotype, not seen; US! – isotype). [TLC: no medullary substances, usnic acid (isotype).]

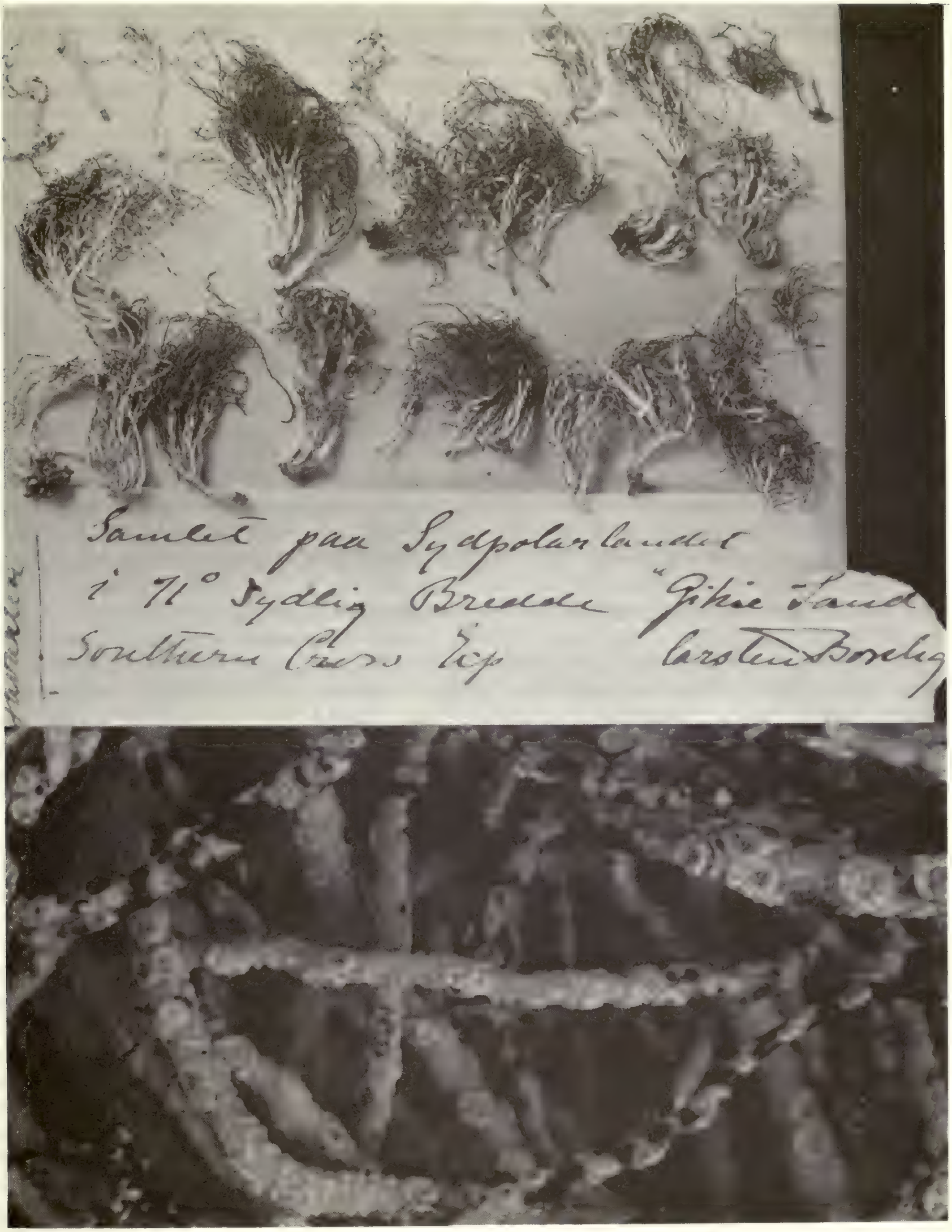
Note 1: *Usnea sulphurea* var. *granulifera* Vainio

This taxon was based on four paratype collections, some of which were later further subdivided, in herb. Vainio (TUR). Although Lamb (1939*a*) illustrated part of herb. Vainio 360 as the type it does not appear that the taxon was formally lectotypified. A small part of this collection in BM! was later annotated as isotype by Lamb. Motyka (1936) referred to material from Île Auguste as being from the *locus classicus* but did not indicate which Vainio specimen was the type. This locality is cited by Vainio under *Racovitza* 208 p.p., which in herb. Vainio is represented by numbers 359, 360, and 361. Consequently later formal lectotypification by Dodge (1973) must be recognised. It is clear that Dodge did not examine all the paratype collections since he selected herb. Vainio 358 (Cap Anna Osterrieth) on the grounds of this being the only fertile material, which is not the case. Herb. Vainio 358 is a mixture of *U. aurantiaco-atra* and fertile *U. antarctica*. It is assumed that Dodge based his lectotypification on *U. antarctica* and that a duplicate specimen in herb. Dodge also belongs to the species. Other paratypes examined belong to *U. antarctica*.

Note 2: *Usnea subfoveolata* Dodge

The systematic position of this taxon remains uncertain. Dodge (1948) regarded the species as being somewhat intermediate between *U. frigida* (= *U. sphacelata*) and *U. antarctica*, since it morphologically resembles the former species but its anatomy was closer to the latter. Type material, from Queen Mary Land, has not been made available but was examined by Lamb in MO (Lamb, 1964), who considered it to be nearer to *U. antarctica*. Material from the type locality in AD has been examined and is nearer to *U. sphacelata*, along with additional specimens in US, possibly determined by Dodge's student. Examination of a photograph of the type specimen (Lamb, unpublished notes, AAS!) shows some affinities with *U. antarctica*, although examination of the actual specimen is required for the systematic position to be finally ascertained.

Description: Thallus (1·5)–2–5(–7–10) cm, arising from a ± delimited, rarely pigmented, holdfast, erect, ± dichotomous, richly branched above with numerous, attenuate branches, rarely with fibrils. Branches terete, yellow-green, ± variegated above with bands of black to violaceous black pigment, ± continuously pigmented towards the apices. Cortex variable in thickness. Surface matt, subpapillate to grossly papillate, papillae usually unpigmented, black-edged annulations absent. Medulla compact, axis thick, occupying 0·5 to 0·7 of the branch diameter. Soralia ± extensive throughout thallus, plane to excavate, rarely pulvinate, arising from papillae, delimited, often with a distinct crateriform margin. Soredia granular, unpigmented, rarely partially corticate then pigmented. Pseudoisidia rare, isidia absent. Apothecia rare, subterminal, as in *U. aurantiaco-atra*. Pycnidia not seen. TLC: (1) fumarprotocetraric acid, ± protocetraric acid, ± cph-1, ± UV+ unknowns, usnic acid; (2) norstictic acid, salazinic acid, usnic acid; (3) no medullary substances, ± UV+ unknowns, usnic acid.


Samlet paa Sydpolarlandet
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Southern Cross Exp
Carsten Borchg

Fig. 13 *Usnea antarctica*. Top. Isotype of *Usnea antarctica* Du Rietz (O) ×1. Bottom. Detail of soralia. South Shetland Is., *Lindsay* 471 (BM) ×10.

Distinguishing features: *Usnea antarctica* is characterised by its erect habit, a richly branched thallus arising from a delimited holdfast, pigmented towards the apices, a grossly papillate surface, a compact medulla, a thick axis, and numerous, plane, discrete, more or less marginate soralia. It is the only asexual species of the subgenus known to occasionally contain fumarprotocetraric acid.

Distribution: *Usnea antarctica* is a circumpolar antarctic species which has its main centre of distribution in the region of the Antarctic peninsula and the associated islands of the Scotia Arc. It also occurs on the subantarctic islands, for example: Bouvetøy, Kerguelen, Macquarie, and Marion, and is rare in the Andes of southern South America (Lamb, 1964) as well as at high altitudes in New Zealand (Mark & Bliss, 1970; Martin & Child, 1972). The species is less frequent in continental Antarctica (Dodge, 1962; Dodge & Baker, 1938; Filson, 1966, 1974; Lamb, 1964; Øvstedal, 1983) whilst it is the only asexual species of the subgenus on the South Shetlands, South Sandwich Islands, Bouvetøy, Îles Kerguelen, Heard Island, Mc.Donald Islands, Marion Island, Macquarie Island, and South Georgia. Fig. 4.

Chemistry: Thalli lacking medullary substances (Race 3) are most frequently encountered overall, whilst those containing fumarprotocetraric acid (Race 1) predominate, or are often the only race, in the subantarctic regions. Both Races 1 and 3 occur on the Antarctic peninsula, although Race 3 extends further south and is the only race found in continental Antarctica. Most South American specimens belong to Race 1 and any depsidone deficient material should be checked against *Usnea patagonica* and analysed by TLC for fatty acids. The presence of occasional traces of unidentified fatty acids in a few specimens of *U. antarctica* is not considered to be significant.

Thalli containing high concentrations of fumarprotocetraric acid were initially regarded as a separate form, f. *sorediifera*, by Lamb (1939*a*). Traces of salazinic acid were occasionally detected in Race 1 whilst the existence of a norstictic and salazinic acid-containing race (Race 2) occurs in the only specimen known from the Falkland Islands. UV+ unknowns, identical to those found in *U. perpusilla*, occur sporadically in Races 1 and 3. Psoromic acid has not yet been demonstrated; previous reports (Golubkova & Schapiro, 1970; Lamb, 1939*a*) correspond respectively to an UV+ unknown and low concentrations of fumarprotocetraric acid that give a PD+ yellow reaction but are not detectable by TLC (BM!).

Variation: Lamb (1939*a*) considered *Usnea antarctica* to be one of the most variable species of the subgenus and discussed the problems involved in selecting suitable characters for delimiting the species. Frequently not all the distinguishing features are developed. However, the species can usually be separated from other asexual species solely on features of the cortex and soralia.

Thallus size and extent of branching are variable, although the thallus almost always arises more or less dichotomously from a delimited holdfast. Secondary branching may be extensive with the production of numerous, relatively short, fine branches. Thalli may rarely become subdecumbent when growing in exposed situations or amongst bryophytes.

The degree of violaceous black pigmentation is generally more extensive in richly branched specimens whilst in some instances pigment may be confined to branch apices or cortical fragments in the soralia. Pigment is usually lacking on primary branches, whilst the area above the holdfast is rarely pigmented. Primary branches are characterised by the presence of conspicuous unpigmented papillae. Papillation is sometimes very reduced particularly in smaller thalli, giving an almost faveolate or subfaveolate appearance. In such rare instances the thallus may have a slightly waxy lustre, rather than more characteristically dull or matt, thus resembling some forms of *Usnea sphacelata*. In these specimens the soralia tend to be very small and their margins become less prominent, or may even be lacking if the surface is exceptionally smooth. This modification has led to the description of several taxa which are here reduced to synonymy, although the interpretation of some of these has been difficult in the non-availability of holotype material. For example, *U. pustulata* represents an extensively sorediate form with a thin, compact, medulla, and an almost smooth, somewhat waxy, surface. From examination of material from near the type locality (AD!) and an unpublished photograph of the holotype taken by Lamb (AAS!), it is clear that this taxon agrees in all details with *U. antarctica*, although *U. sphacelata* also occurs in a mixed collection from Possession nunatak made by Borchgrevink (UPS!).

Usnea subfoveolata and *U. subpapillata* were both described from the same locality. From examination of additional cited specimens (AD!) of both species from the type locality, it is evident that Dodge's original concepts (Dodge, 1948) of the taxa included some specimens of *U. sphacelata*. However, following Lamb's observations (Lamb, 1964) on the type specimens and examination of his unpublished photographs (AAS!), it is likely that the type material of both taxa is closer to *U. antarctica*.

The pale patches in the cortex of the type of *Usnea insularis* appear to be the result of erosion combined with incipient soralia formation, rather than maculae formed as a result of extension of the axis through the cortex as in *U. taylorii*. This type has been compared with *U. antarctica* from Îles Kerguelen which has a similar eroded cortex and only a few, small papillae.

Thallus anatomy is constant in as far as the axis usually occupies half or more of the diameter in main branches and the medulla remains densely interwoven, at least towards the cortex. A very wide range of variation occurs in the relative widths of each tissue, particularly amongst robust populations from Îles Kerguelen and Marion and Prince Edward Islands. Such development has formed the basis for the description of a wide range of taxa that can no longer be regarded as distinct. For example, *Usnea crassa* is a very robust form of the species originally distinguished by an exceptionally thick axis, that is irregular in outline, and possesses a small central cavity, as well as a very thick cortex. The original description gives measurements of up to 260 μm for the cortex, which presumably includes prominent papillae, since the maximum width for isotype material is *c.* 170 μm, whilst *c.* 100 μm is more usual in specimens from the Antarctic peninsula. Similarly *U. pseudofruticosa* was separated on slight differences in thickness of cortex, medulla, and axis.

Robust material of Race 1 from Heard Island and Îles Kerguelen was reported to have a partially sub-divided axis like *Usnea taylorii* and recognised as a distinct species, *U. insularis* (Dodge, 1948; Lamb, 1939*a*; Lindsay, 1977*b*). Occasionally thalli examined from these locations, and also from Marion Island, have axes with a small central lumen and slightly irregular outline, but I have not found any thalli with a distinctly divided axis. *U. crombiei* was distinguished for similar reasons, although the original material indicates that the slight invagination of the axis is not particularly pronounced.

Papillae give rise to soralia throughout the thallus which may extend down main branches, rather than remaining confined to apices as in *Usnea sphacelata*. In robust thalli, with large papillae, the soralia are very characteristic since papillae from which they are derived form a distinctive crateriform margin. Soralia are usually unpigmented, plane to slightly concave-excavate, rarely convex, and smaller than the branch diameter, although they may become confluent on ultimate branches, a feature that is sometimes characteristic of Race 1 from the subantarctic regions. In southern South America a wider range of variation of form of soralia occurs. Sometimes small pseudoisidia are produced in the soralium, but these are never as large or distinct as in *U. durietzii* or *U. patagonica*. Other variations include small, plane soralia in more extensively pigmented thalli with fibrils; globular, pigmented soralia are characteristic of a few thalli all belonging to Race 1 which also have a slightly lax medulla and were found in a mixed collection with *U.* cf. *subantarctica* (*Santesson* 641c, S!). When damaged, small, spinule-like projections, may be produced from soralia (*Santesson* 637a, S!); this was regarded as a distinctive feature in *U. propagulifera* by Dodge (1948).

Fertile material (Fig. 14) of *Usnea antarctica* is rare and apothecia are only produced in areas of optimum luxuriance, for example, the type of *U. floriformis* from Heard Island. Lamb (1939*a*, 1948*a*, 1964) reported fertile material from the Antarctic peninsula, South Georgia, and Tierra del Fuego. In addition, fertile material belonging to Races 1 and 3 has now been found amongst collections from the South Orkneys, South Shetlands, South Sandwich Islands, and Bouvetøy; the only Falkland Island specimen (Race 2) also bears rudimentary apothecia. The apothecia are subterminal or lateral, or are sometimes produced in series along a single branch. They are usually small, cupular, or rarely expanded with an irregular to crenulate margin. The disc is

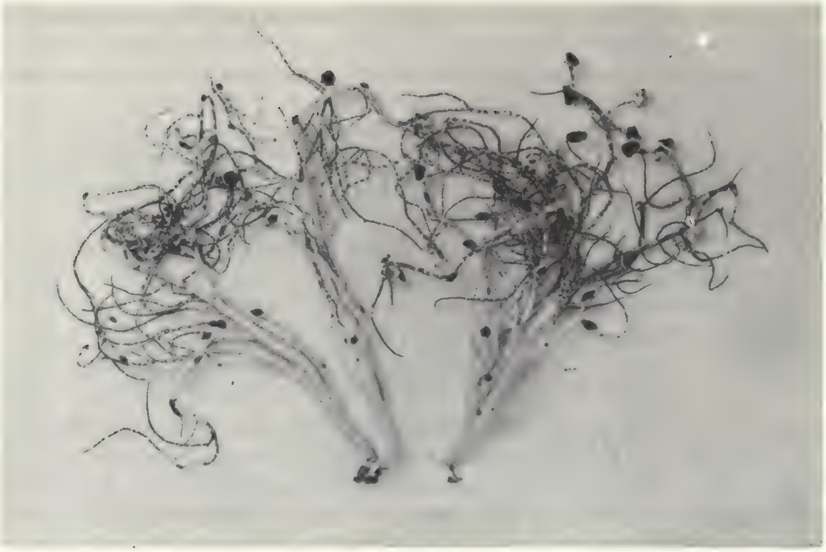


Fig. 14 Fertile thalli of *Usnea antarctica*. Antarctic peninsula, Anvers I., *Lamb* 8025 p.p. (FH) ×1.

black or rarely brown when immature. In fertile specimens soralia may be either abundant or scarce. One specimen (Race 1) from South Georgia (*Lindsay* 4327, AAS!) bears a superficial resemblance to *U. ciliata* in habit but has a verrucose surface and very scanty development of soralia.

Species concept: The wide range of variation found in *Usnea antarctica* has led to the description and recognition of a number of species by various authors according to their particular species concepts (see synonymy), all of which here fall within the variation of the species.

The holotype specimen of *Usnea antarctica* represents a less robust form and in some respects has some features in common with *U. sphacelata*. The thalli have a slightly lax medulla, slender, variegated secondary branches, are subpapillate, and have small, plane, eroded soralia, sometimes lacking the distinctive margin.

It is surprising that *Usnea antarctica* was not recognised as a distinct species before Du Rietz' treatment (Du Rietz, 1926) of the subgenus; this taxon previously being included as a variety of *U. sphacelata*. Du Rietz (1926) based the species on two varieties previously assigned to *U. sulphurea*. Of these *U. sulphurea* var. *granulifera* is more typical of populations from the Antarctic peninsula and var. *sorediifera* representative of richly sorediate material of Race 1 form Îles Kerguelen.

Usnea antarctica is very probably the sorediate counterpart of *U. aurantiaco-atra*. Supporting evidence for this comes from the similarity of surface ornamentation and apothecia as well as from chemical data. The existance of three chemical races in the two species with similar distributions in South America and Antarctica lends support to this theory, in particular the validity of the single specimen of Race 3. This sorediate specimen is unique and was probably the result of a sporadic secondary formation from the norstictic-salazinic race of the fertile counterpart, on the Falkland Islands. It is unlikely that the specimen is misplaced since the remaining two specimens in the same herbarium packet belong to the norstictic-salazinic race of *U. aurantiaco-atra* which also has a restricted distribution (see p. 69).

In areas where the distributions overlap, *Usnea antarctica* may be distinguished from *U. sphacelata* and *U. subantarctica* by the marginate soralia arising from large, unpigmented papillae, a compact medulla and broad axis; from *U. durietzii* and *U. patagonica* (Table 3) by differences in habit, basal pigmentation, a compact medulla, and absence of pseudoisidia; from *U. neuropogonoides* by habit and presence of soralia; and from *U. acromelana* and *U. pseudocapillaris* by the presence of papillae and lack of annulations, and sometimes also by chemical differences.

Selected specimens examined
Race 1

CHILE. Magellanes: Mt. Aymond, Straits of Magellan, 1872, *Hassler Exped.* s.n. (BM, FH, PC); Isla Navarino, Puerto Navarino, 10 m, 28 February 1940, *R. Santesson* 1234b (S); Tierra del Fuego, San Sebastian, 2 January 1896, *P. Dusén* 80 (BM); Canal Beagle, Yendegaia, by glacier, 50–100 m, 4 March 1940, *R. Santesson* 1373 p.p. (UPS).

ARGENTINA. Santa Cruz: Cordillera Darwin, Cerro Mayo, above Seno Mayo, Lago Argentino, *c.* 1000 m, February 1959, *P. W. James* 73 (BM), near front of Ventrisquero Mayo, 90 m, March 1959, *P. W. James* 5052 (BM). Tierra del Fuego: Sierra Alvear, S. slope, above Las Cotorras, (*c.* 20 km ENE. of Ushuaia), 700 m, 9 February 1940, *R. Santesson* 637a (S, UPS), Sierra Sorondo, N. slope, above Las Cotorras, 800 m, 6 February 1940, *R. Santesson* 641*c.* p.p. (S).

SOUTH GEORGIA. Cumberland East Bay, above Hope Point, 80 m, January 1973, *D. C. Lindsay* 4327 (fertile) (AAS); Whale Valley, 250 m, January 1973, *D. C. Lindsay* 3957 (fertile) (AAS); Royal Bay, 29 April 1902, *C. Skottsberg* s.n. (S); N. of Sandebugten, W. shore of Barff Peninsula, *c.* 15 m, 14 January 1961, *S. W. Greene* 939 (AAS, BM).

SOUTH ORKNEY IS. Signy I.: Paal Harbour, 90 m, 2 April 1965, *R. I. L. Smith* 429 (AAS); Tern Cove, 15 m, 24 October 1973, *T. N. Hooker* 263 (fertile) (AAS). Coronation I.: Top of Wave Peak Buttress, 392 m, 29 September 1973, *T. N. Hooker* 194 (AAS). Laurie I.: Cape Dundas, 60 m, 15 February 1971, *M. McManmon* 195 (AAS).

SOUTH SHETLAND IS. King George I.: Admiralty Bay, Keller Peninsula, 24 December 1960, *B. J. Taylor* 324 (AAS), 50–60 m, 5 January 1953, *B. Frödin* 21a (UPS).

ANTARCTIC PENINSULA. Graham Land: Joinville I. [63°15′S: 55°48′W], Mt. Alexander, 200–500 m, 27 March 1981, *R. I. L. Smith* 3680 p.p. (AAS); Trinity Peninsula, Hope Bay [63°23′S: 57°00′W], 105 m, 16 April 1945, *F.I.D.S.* D2375 p.p. (BM), Duse Bay [63°32′S: 57°15′W], 370 m, 6 January 1946, *E. H. Back* F.I.D.S. D2865 (BM); Palmer Archipelago, Wiencke I. [64°48′S: 63°25′W], N. buttress of Noble Peak, *c.* 210 m, 15 October 1944, *I. M. Lamb* Operation Tabarin 1307 (BM); Argentine Is., Galindez I. [65°15′S: 64°15′W], 27 December 1935, *B.G.L.E.* 1328-2 (BM); Fallières Coast, Adelaide I. [*c.* 67°60′S: 68°20′W], nunatak *c.* 18 km N. of base hut [Rothera], 10 December 1962, *F. Gibbs* Killingbeck 207b (AAS, BM).

MARION I. Tafelberg, E. slope, *c.* 320 m, 10 May 1982, *H. Hertel* 24 593 (M); Skua's Ridge, 80 m, 26 January 1972, *A. de Villers* 4-31 (BLFU); Johnny's Hill, 4 January 1951, *R. W. Rand* 3310 (BOL).

PRINCE EDWARD I. vicinity of Kent Crater, *c.* 50 m, 1 May 1982, *H. Hertel* 24 343 (M).

ÎS. KERGUELEN. Cliffs above Lake du Val Studer, 11 February 1963, *R. B. Filson* 4665 p.p. (BM); Royal Sound, 1897–98, *R. Hall* s.n. (MEL 9230).

HEARD I. between Rogers Head, Corinthian Bay, West Beach, and the foot of the glacier from Big Ben (Kaiser Wilhelm Peak), 28 November–2 December 1929, *B.A.N.Z.A.R.E.* B140–43 (AD).

MC.DONALD IS. 13 March 1980, *J. Jenkin* s.n. (herb. Seppelt 11123).

MACQUARIE I. between North Mount and Handspike Point, 7 December 1968, *D. McVean* 6909 (BM); Perseverance Bluff, 100 m, 29 January 1982, *R. D. Seppelt* 12748 (herb. Seppelt).

NEW ZEALAND. Canterbury: Kirkliston Range, 1680–1830 m, 25 March 1978, *D. J. Galloway* s.n. (BM, CHR 343299). Otago: Mt. Pisa, 1920 m, March 1968, *D. J. Galloway* s.n. (CHR 343771); Mt. Earnslaw, 2240 m, May 1961, *R. G. Cunninghame* s.n. p.p. (BM, OTA); Old Man Range, *c.* 1370 m, 1 February 1963, *P. W. James* 1159 p.p. (BM).

Race 2

FALKLAND IS. (unlocalised), 1824, Greville herb. (E).

Race 3

SOUTH GEORGIA. Cumberland West Bay, Bore Valley, 105 m, 11 February 1961, *S. W. Greene* 1979 (AAS, BM, FH); Cumberland East Bay, Dartmouth Point, 30 m, 5 December 1971, *D. C. Lindsay* 3458 (BM); 1921–22 *Shackleton-Rowett Exped.* 10 p.p. (BM).

SOUTH SANDWICH IS. Candlemas I.: 180 m, 5 March 1964, *R. E. Longton* 535 (fertile) (BM). Bellinghausen I.: 200 m, 10 March 1964, *M. W. Holdgate* 825c (AAS, BM). Visokoi I.: Finger Point, 6 m, 9 January 1961, *K. Archibald* 35 (AAS, BM, FH).

SOUTH ORKNEY IS. Signy I.: Borge Bay, Knife Point, 9 m, 8 October 1966, *D. C. Lindsay* 1255 (BM); Observation Bluff, 60 m, 21 January 1972, *T. N. Hooker* 1 (AAS). Laurie I.: Scotia Bay, 11 March 1953, *A.*

E. Hunziker 10238 (FH). Powell I.: between Cape Disappointment and Falkland Harbour, 30 m, 30 January 1965, *R. I. L. Smith* 263 (AAS, BM).

SOUTH SHETLAND IS. King George I.: Admiralty Bay, mountain slope between Petrified Forest Creek and Ornithologist's Creek, 100 m, 26 December 1979, *R. Ochyra* 5000/79 (M). Deception I.: Kroner Lake, 30 January 1960, *B. J. Taylor* 29 (AAS, BM). Robert I.: 1963, *G. Follmann* 17441 (KASSEL).

ANTARCTIC PENINSULA. Graham Land: Joinville I. [63°15′S: 55°45′W], Active Sound, 200 m, 27 March 1981, *R. I. L. Smith* 3735 (AAS); Palmer Archipelago, Anvers I. [64°45′S: 64°05′W], Arthur Harbour, Palmer Station, 10 m, 4 February 1965, *I. M. Lamb* Operation Tabarin 8025 p.p. (fertile) (FH); Marguerite Bay, Jenny I. [67°44′S: 68°25′W], 9 m, 17 October 1948, *B. Stonehouse & V. E. Fuchs* F.I.D.S. E466-1a (BM).

DRONNING MAUD LAND. [*c.* 15°W]. Vestfjella, Basen, *c.* 300 m, 1968–69, *A. Hjelle* s.n. (O).

EDWARD VII LAND. [*c.* 150°W]. Rockefeller Mountains, Mt. Marguerite Wade, 17 December 1940, *R. G. Frazier & F. A. Wade* U.S.A.S. 320 (US).

VICTORIA LAND. [*c.* 165°E]. Geikie Land, 300 m, 1900, *Southern Cross Exped.* s.n. (BM); Hallett Peninsula, *c.* 300 m, 11 November 1962, *E. D. Rudolph* 62040 (LD).

GEORGE V LAND. [*c.* 150°E]. Dreadnought or Horn Bluff, 21 December 1912, *A. L. McLean* A.A.E. 46 (AD).

KNOX COAST. [*c.* 110°E]. Mitchell Peninsula, outcrop 1·5 km E. of Pidgeon I., 21 December 1982, *R. D. Seppelt* 013357 (herb. Seppelt).

QUEEN MARY LAND. [*c.* 95°E]. Alligator Nunatak, 2 January 1913, *C. T. Harrisson* A.A.E. 72 (AD).

KAISER WILHELM II LAND. [*c.* 90°E]. Haswell I., 20 December 1957, *V. Rozov* 101 (AAS, FH).

MAC.ROBERTSON LAND. [*c.* 70°E]. Tschuffert Peak, 9 February 1974, *R. Filson* 14900 Lich. Ant. Exs. 23 (AAS, BM, M, O); Hays Peak, Cape Bruce, 10 October 1962, *R. Filson* 4387 (AAS).

MAC.ROBERTSON–ENDERBY LAND TRAVERSE. [*c.* 60°E]. 1964–65, *N. Leid* Bratt 3272a (HO 35190).

BOUVETØY. Rustadkollen, 340 m, 7 March 1979, *T. Engelskjön* s.n. (BG, BM); S. of Kapp Circoncision, *c.* 15 m, 31 March 1964, *M. W. Holdgate* 868a (AAS, BM, FH).

MARION I. 26 December 1873, *Challenger Exped.* s.n. (type of *U. insularis* Lamb) (BM).

HEARD I. Dreadnought (Horn) Bluff, 21 December 1912, *A. L. McLean* A.A.E. 46 (AD).

MACQUARIE I. Wireless Hill, 90 m, 8 December 1968, *D. McVean* 6907 (BM); near Lake Scoble, 7 December 1968, *D. McVean* 6935 (BM); Green Gorge, 220 m, 26 October 1983, *R. D. Seppelt* 14297 (herb. Seppelt).

The following may be consulted for further localities: South Georgia (Lindsay, 1974), South Sandwich Is. (Longton & Holdgate, 1979), South Orkney Is. (Smith, 1973), South Shetland Is. (Lindsay, 1971*a*), Antarctic Peninsula (Lamb, 1964); together with lists held in BM and collections in AAS and BM.

4. **Usnea aurantiaco-atra** (Jacq.) Bory **Figs 15–19**

in *Mém. Soc. Linn. Paris* **4**: 596 (1826). – *Lichen aurantiaco-ater* Jacq., *Miscell. Austriac.* **2**: 369 (1781). – *Neuropogon aurantiaco-ater* (Jacq.) Lamb in *J. Linn. Soc.* (Bot.) **52**: 221 (1939). Type: [Chile] Magellan Straits, 1767, *Commerson*, comm. D. Jussieu (PC! – lectotype, selected here; BM!; FI!, LINN (herb. Smith 1715.9)!, UPS (herb. Thunberg 26355)! – isolectotypes). [TLC: fumarprotocetraric acid aggr., usnic acid.] (see Note 1)

Usnea melaxantha Ach., *Method Lich.*: 307 (1803). – *Parmelia melaxantha* (Ach.) Sprengel, *Syst. Veg.* **4** (1): 277 (1827). – *Neuropogon melaxanthus* (Ach.) Nyl. in *Mém. Soc. Imp. Sci. Nat. Cherbourg* **3**: 170 (1855). Type: America [West Falkland Is.], Port Egmont, *Cavanilles*, Ach. 1887A (H-ACH! – lectotype; BM! – isolectotype). [TLC: norstictic acid, salazinic acid, connorstictic acid, protocetraric acid (trace), usnic acid.] (see note 2)

Usnea fasciata Torrey in *Am. J. Sci.* **6**: 106 (1823). – *Usnea melaxantha* var. *γ fasciata* J. D. Hook., *Flora Antarctica* **2**: 520 (1847). Type: New South Shetland, comm. Dr. Mitchill (NY! – lectotype, selected here). [TLC: fumarprotocetraric acid, protocetraric acid (trace), usnic acid.] (see Note 3)

Cornicularia flavicans Pers. *in* Gaudichaud *in* Freycinet, *Voyage autour du Monde, Botanique*: 210 (1828). Type: Îles Malouines [Falkland Is.], 1820, *C. Gaudichaud* 130 (PC! – holotype; G-DEL! – isotype; BM! – ?isotype). [TLC: norstictic acid, salazinic acid, protocetraric acid (trace), usnic acid.]

Neuropogon antennarius Nees & Flotow in *Linnaea* **9**: 497 (1835). – *Usnea antennaria* (Nees & Flotow) Massal., *Memor. Lichenogr.*: 73 (1853). Type: ad rupes Chil. austr. in summo cacumine Pico de Pilque prope Antuco [37°20′S: 71°41′W], legit *Poeppig*, ex herb. Kunze (VER (herb. Massalongo)! – lectotype, selected here). [TLC: norstictic acid, salazinic acid, usnic acid.] (see Note 4)

Usnea melaxantha var. *α Acharii* J. D. Hook., *Flora Antarctica* **2**: 520 (1847); nom. illeg. (Article 26.1).

Usnea melaxantha var. *β Jacquinii* J. D. Hook., *Flora Antarctica* **2**: 520 (1847). Type: *Lichen aurantiaco-ater* Jacq.

Usnea melaxantha var. *subciliata* Zahlbr. in *Annls mycol.* **1**: 360 (1903). – *Usnea sulphurea* var. *subciliata* (Zahlbr.) Zahlbr., *Cat. Lich. Univ.* **6**: 603 (1930). – *Neuropogon strigulosus* f. *subciliatus* (Zahlbr.) Lamb in *J. Linn. Soc.* (Bot.) **52**: 231 (1939). Type: Patagonia, *P. Neumann* (W7177! – holotype). [TLC: fumarprotocetraric acid (trace), usnic acid.]

Usnea melaxantha var. *subciliata* f. *strigulosa* Zahlbr. in *Annls mycol.* **1**: 360 (1903). – *Usnea melaxantha* f. *strigulosa* (Zahlbr.) R. H. Howe in *Bryologist* **18**: 61 (1915). – *Usnea sulphurea* var. *subciliata* f. *strigulosa* (Zahlbr.) Zahlbr., *Cat. Lich. Univ.* **6**: 603 (1930). – *Usnea strigulosa* (Zahlbr.) Motyka, *Lich. Gen. Usn. Stud. Monogr.* **1**: 30 (1936). – *Neuropogon strigulosus* (Zahlbr.) Lamb in *J. Linn. Soc.* (Bot.) **52**: 229 (1939). – *Neuropogon aurantiaco-ater* f. *strigulosus* (Zahlbr.) Lamb in *Lilloa* **14**: 152 (1948). – *Usnea aurantiaco-atra* f. *strigulosa* (Zahlbr.) Lamb in *An. Parq. nac. B. Aires* **7**: 156 (1959) ['1958']. – *Usnea fasciata* f. *strigulosa* (Zahlbr.) Lamb in *Br. Antarct. Surv. Sci. Rep.* **38**: 14 (1964). Type: Patagonia, *P. Neumann* (W7116! – holotype). [TLC: ± fumarprotocetraric acid, ± protocetraric acid, ± UV+ unknowns, usnic acid.]

Usnea sulphurea var. *normalis* Vainio, *Rés. Voy. S. Y. Belgica, 1897–99, Botan., Lichens*: 11 (1903) nom. inval. (Article 26.1). – *Neuropogon aurantiaco-ater* f. *normalis* Lamb in *J. Linn. Soc.* (Bot.) **52**: 224 (1939) nom. inval. (Article 26.1.).

Usnea sulphurea var. *normalis* f. *activa* Zahlbr. in *K. svenska VetenskAkad. Handl.* **57** (6): 44 (1917). – *Usnea sulphurea* f. *activa* (Zahlbr.) Zahlbr. *Cat. Lich. Univ.* **6**: 603 (1930). Type: Falkland Inseln, Port Stanley, Sapper Hill, *Schwedische antarktische Exped. 1901–03.* (W 123 ! – holotype). [TLC: norstictic acid, salazinic acid, usnic acid.]

Usnea sulphurea var. *spadicea* Zahlbr. in *K. svenska VetenskAkad. Handl.* **57** (6): 45 (1917). – *Usnea taylorii* var. *subspadicea* (Zahlbr.) Motyka *in* Räsänen in *Suomal. eläin-ja kasvit. Seur. van. kasvit. Julk.* **2**(1): 11 (1932) nom. illeg. (Article 63.1). – *Usnea melaxantha* var. *spadicea* (Zahlbr.) Motyka, *Lich. Gen. Usn. Stud. Mongr.* **1**: 35 (1936). – *Neuropogon melaxanthus* f. *spadiceus* (Zahlbr.) Lamb in *J. Linn. Soc.* (Bot.) **52**: 228 (1939). Type: Falkland Inseln, Mt. Adams, Schwedische antarktische Exped. 1901–03, *C. Skottsberg.* (W121! – holotype). [TLC: norstictic acid, salazinic acid, usnic acid.] (see Note 5)

Usnea melaxantha var. *nigropallida* Cengia-Sambo in *Boll. Soc. bot. ital.* **1**: 91 (1926). – *Neuropogon aurantiaco-ater* f. *nigropallida* (Cengia-Sambo) Lamb in *J. Linn. Soc.* (Bot.) **52**: 224 (1939). Type: Tierra del Fuoco, 1913, *G. B. de Gasperi* (FI! – holotype; FI! – isotype). [TLC: fumarprotocetraric acid, protocetraric acid, usnic acid.]

Usnea taylorii var. *kranckii* Räsänen in *Suomal. eläin-ja kasvit. Seur. van. Julk.* **2**(1): 10 (1932). Type: [Chile] Fuegia occ. Fjordo Martinez, Seno Plüschow, *c.* 500 m.s.m., reg. alp., Expeditio Fennica 1928–29, 21 February 1929, *E. H. Kranck* (H! – lectotype, selected here). [TLC: fumarprotocetraric acid, protocetraric acid, usnic acid.] (see Note 6)

Usnea trachycarpa var. *eciliata* Räsänen in *Suomal. eläin-ja kasvit. Seur. van kasvit Julk.* **2**(1): 10 (1932). Type: [Chile] Fuegia occ. Puerto Yartou, Pico Nariz, 750 m.s.m., reg. alp. Expeditio Fennica 1928–29, *H. Roivainen* (H! – holotype; S – isotype, not seen). [TLC: norstictic acid, salazinic acid, protocetraric acid (trace), usnic acid.]

Usnea aurantiaca Motyka, *Lich. Gen. Usn. Stud. Monogr.* **1**: 29 (1936). – *Neuropogon aurantiacus* (Motyka) Lamb in *J. Linn. Soc.* (Bot.) **52**: 229 (1939). Type: Falkland Is., *D. Coleman,* A. Zahlbr. Lich. Rar. Exs. 20 (W5133! – holotype; UPS! – isotype). [TLC: norstictic acid, salazinic acid, protocetraric acid (trace), usnic acid.]

Neuropogon aurantiaco-ater f. *egentissimus* Lamb in *J. Linn. Soc.* (Bot.) **52**: 225 (1939). – *Usnea aurantiaco-ater* f. *egentissima* (Lamb) Dodge, *Lich. Fl. Antarct. Cont.*: 227 (1973). Type: Antarctica, Graham Land, Argentine Is., summit of Galindez I., 2 January 1936, *Br. Graham Land ('Penola') Exped. 1934–37,* 1340j (BM! – holotype). [TLC: no medullary substances, usnic acid.]

Neuropogon melaxanthus f. *fibrillifer* Lamb in *Lilloa* **14**: 154 (1948). Type: Falkland Is., peat moors above Port Stanley, *c.* 60 m, 27 January 1946, *I. M. Lamb,* 'Operation Tabarin' 2873 (BM! – holotype). [TLC: norstictic acid, salazinic acid, protocetraric acid (trace), usnic acid.]

?*Usnea siplei* Zammuto *in* Dodge in *Trans. Am. microsc. Soc.* **84**: 522 (1965). Type: Antarctica [Graham Land], Melchior Is., Omega I. [= Lystad I.], 64°20′S: 62°56′W, 14 March 1941, *P. A. Siple* 367 (herb. Dodge – holotype, not seen; US! – isotype). [TLC: fumarprotocetraric acid aggr., UV+ unknowns, usnic acid.] (see Note 7)

Note 1: *Lichen aurantiaco-ater* Jacq.

(i) The hyphen should be retained in accordance with Article 73.1.

(ii) There has been considerable confusion concerning the correct identity of this taxon. The holotype specimen has not been traced and Jacquin's personal lichen herbarium in Vienna is regarded as lost (Motyka, 1936; Lamb, 1939*a*). Consequently assumptions have been made as to the medullary chemistry of the type specimen. This has resulted in subsequent changes in use of various specific epithets, all of which are here regarded as synonyms (Table 4).

Jacquin (1781) based the name *Lichen aurantiaco-ater* on material collected by Commerson, probably from the Magellan Straits. Examples of Commerson's collections have been traced in several herbaria and, since they presumably originated from PC, are regarded as isotypes. Two collections have been traced in PC of which one (herb. Jussieu !) very closely conforms with Jacquin's original illustration (Tab XI, fig. 2) and description. This specimen is accordingly designated here as the lectotype (Fig. 15), with isolectotypes selected in other herbaria. The specimen contains fumarprotocetraric acid which follows Lamb's original concept (Lamb, 1939*a*) of the type. Motyka annotated this specimen as *Usnea aurantiaco-atra* although wrongly listing it (Motyka, 1936) under *U. aurantiaca*, with the erroneous date of 1820.

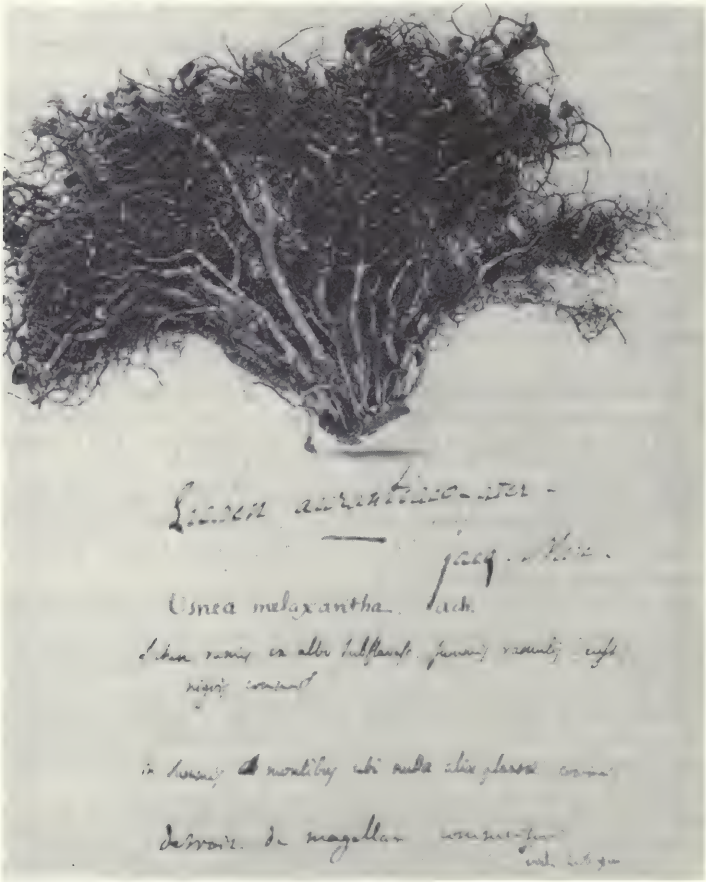


Fig. 15 Lectotype of *Lichen aurantiaco-ater* Jacq. (PC) ×1.

Most of Commerson's collections contain fumarprotocetraric acid, apart from the collection in BM which also includes norstictic and salazinic acid-containing thalli. In this particular case only the fumarprotocetraric acid-containing thalli are selected as isolectotype material. This lectotypification reflects the predominance of Race 1 (see p. 69) in the Magellan Straits area.

Note 2: *Usnea melaxantha* Ach.

The type collection of *Usnea melaxantha* Ach. (Ach. 1887 A + B) consists of two plants from different localities, both containing norstictic and salazinic acids. One gathering, collected by Menzies, is from

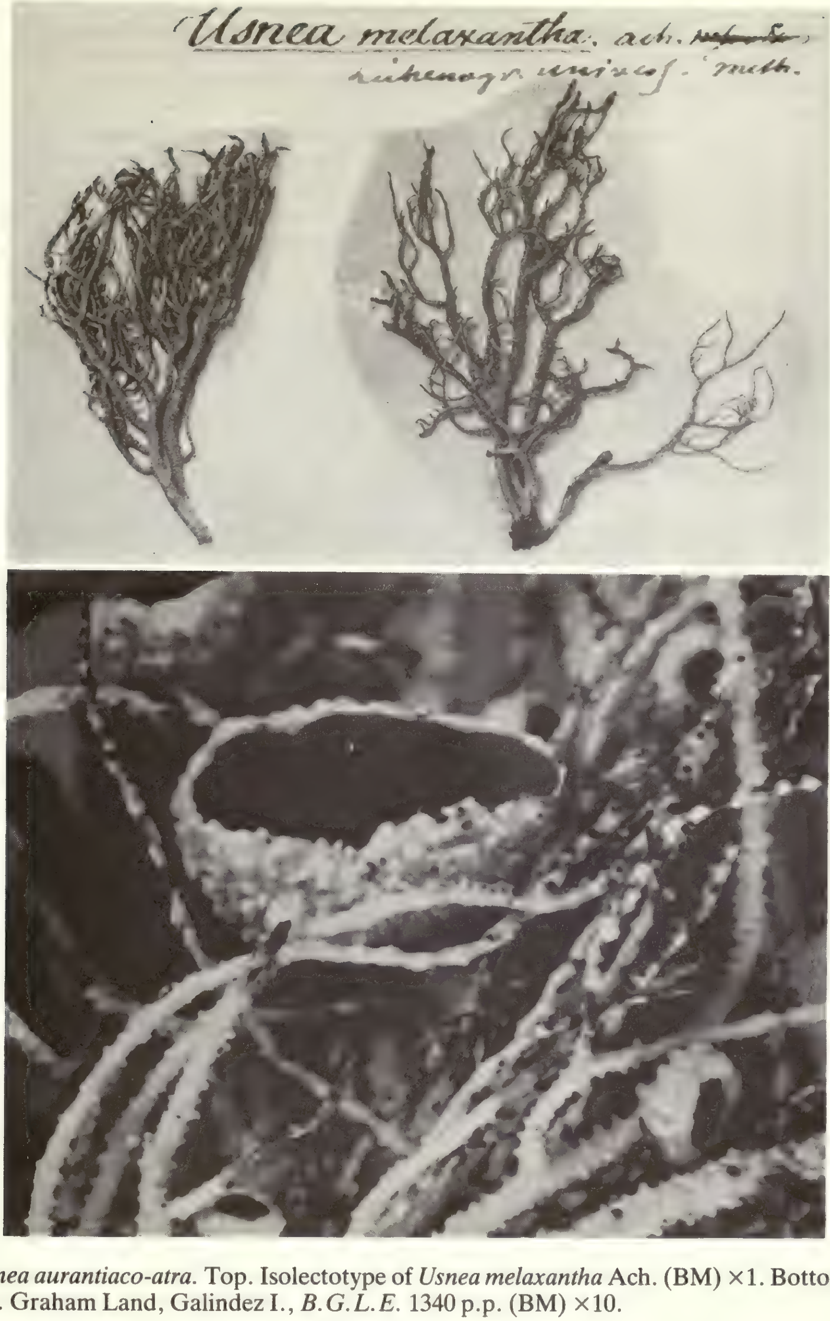


Fig. 16 *Usnea aurantiaco-atra*. Top. Isolectotype of *Usnea melaxantha* Ach. (BM) ×1. Bottom. Detail of apothecia. Graham Land, Galindez I., *B.G.L.E.* 1340 p.p. (BM) ×10.

'Staaten Land' and the other, from the Falkland Islands (Port Egmont), was collected by Cavanilles. Motyka (1936) regarded the Port Egmont specimen as the nomenclatural type from the classic locality. His selection is therefore considered to effect the lectotypification of this taxon. This lectotype is illustrated by Lamb (1939*a*, pl. 11, fig. 28). A duplicate collection in BM (Fig. 16) is recognised as an isolectotype although the two plants are unlocalised.

Note 3: *Usnea fasciata* Torrey
Torrey probably described this taxon on material from two sources; that collected by Captain Napier of the U.S. Sealing Expedition of 1820–21 (Dodge, 1973) and an unknown collector, both of which were sent

to him by Dr S. L. Mitchill (Torrey, 1823). Consequently his description is likely to have been based on a mixed gathering. Lamb (1939*a*) illustrated a fertile specimen of *Usnea aurantiaco-atra* (NY!) as the holotype, but he later (Lamb, 1964) retracted this because Torrey, in his original description, stated that specimens lacked apothecia, only possessing 'cephalodia' which, from study of his illustration, correspond to a lichen parasite.

It is evident, from examination of the herbarium sheet, that Lamb was sent only part of one thallus of the NY collection in a separate capsule. The original collection (Fig. 17), which was not seen by him, bears an inscription in Torrey's handwriting. Consequently, it may be assumed, despite the presence of fertile material, that this material is authentic, especially as the journal citation on the packet lacks specific details. This collection comprises the 'parent' thallus of the fertile specimen sent to Lamb, as well as a sterile thallus of the same species (both lacking parasites) and two small, distinctly variegated, parasitised thalli of *U. antarctica*.

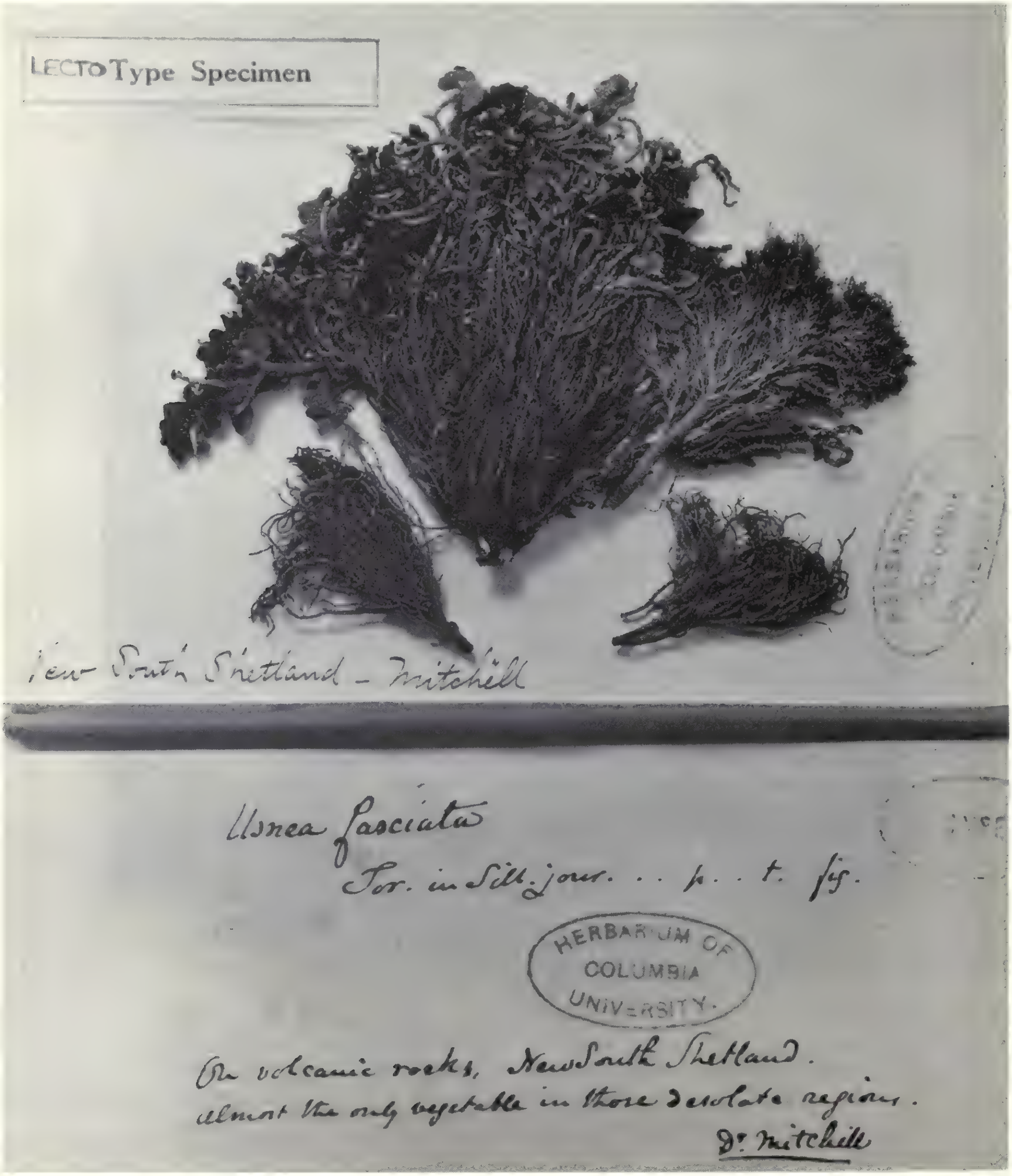

LECTOType Specimen
New South Shetland – Mitchill
Usnea fasciata
Tor. in Sill. jour. . . p. . t. fig.
HERBARIUM OF COLUMBIA UNIVERSITY
On volcanic rocks, New South Shetland.
almost the only vegetable in those desolate regions.
Dr Mitchill

Fig. 17 *Usnea aurantiaco-atra*. Lectotype (centre thallus) of *Usnea fasciata* Torrey (NY) ×1.

Torrey's illustration (Torrey, 1823; pl. 9 figs 1–4) which represents a large, conspicuously variegated thallus, lacking apothecia but clearly parasitised, must be taken into consideration. None of the thalli in the NY collection exactly correspond to this illustration, although the closest are the parasitised thalli of *U. antarctica*, despite difference in size and apparent lack of soralia. There is a remote possibility that Torrey may have misinterpreted the apothecia as well-developed 'cephalodia', since he described them as 'scattered, sometimes crowded and irregular', rather than recognising them as the same fertile structures that occur in the subgenus *Usnea*, although he might have regarded the fertile specimen as an older state of the same species. It is evident from the protologue (Torrey, 1823: 105) that he was fully aware of the distinction between apothecia and 'cephalodia'-like structures in *U. florida* (=? *U. strigosa*).

Consequently there are three options relevant to the typification of *Usnea fasciata* based on this NY collection.

(i) to follow Lamb's final interpretation (Lamb, 1964) and reject the collection as being the type of the name. A neotype would then have to be selected.

(ii) Assume only part of the collection to be the type of the name and lectotypify the parasitised, sorediate material based on comparison with Torrey's illustration. This would result in a change of nomenclature of *U. antarctica*.

(iii) Assume the entire mixed collection to be the type of the name and lectotypify on one element (Article 9:2) so as to preserve current usage, following Recommendation 7B, since the name can no longer be rejected under Article 70.

None of these solutions is entirely satisfactory, but it is important to stabilise the situation and to save further misapplication or nomenclatural changes. Thus *Usnea fasciata* is here lectotypified on the fertile specimen, reducing the taxon to synonymy with *U. aurantiaco-atra* and preventing a confusing name change for *U. antarctica*.

Note 4: *Neuropogon antennarius* Nees & Flotow

Motyka (1936) reported examining the fragmentary holotype specimen in herb. Flotow (B) which was subsequently destroyed during the Second World War (Krog, 1976). Material of various species from the classic locality, collected by Poeppig, was sent to Kunze at Leipzig (Sayre, 1975). Some of these collections were subsequently distributed by Poeppig and Kunze as part of an unpublished exsiccatum, *Poeppig Coll. pl. Chil. N. antennarius* does not form either of the two examples of the exsiccatum that have been traced (BM!), and authentic material has not been found in Poeppig's personal herbarium (W), although collections of *U. perpusilla* from herb. Poeppig and herb. Kunze have been traced in M and PC, annotated *U. fasciata* and *U. melaxantha* respectively.

The only authentic material of *N. antennarius* traced is in herb. Massalongo (VER!) and originates from herb. Kunze. This specimen is presumably an isotype, since, besides bearing the same data as the above exsiccatum, bears the inscription '*Neuropogon antennarius* Nees & Flotow' in Massalongo's handwriting and a small ink stamp he used to denote type material. This collection (Fig. 18) is consequently selected as the lectotype of *Neuropogon antennarius*, following Krog's lectotypification of *N. poeppigii* (Krog, 1976) based on an isotype traced in S.

Note 5: *Usnea sulphurea* var. *spadicea* Zahlbr.

This variety was validly published by Zahlbruckner in 1917, although examination of the type specimen (W 121) indicated that he possibly intended the epithet '*subspadicea*' to be used since this name appears in his handwriting on the label. Motyka in Räsänen (1932) published the combination 'Usnea taylori var. subspadicea (Zahlbr.) Motyka' based on this unpublished name as indicated on his determination label attached to herb. NYL 36372 (H!). As both names are of the same rank 'Usnea taylori var. subspadicea' must be rejected under Article 63.1 as a superfluous name for *Usnea sulphurea* var. *spadicea* Zahlbr.

Note 6: *Usnea taylorii* var. *kranckii* Räsänen

Examination of the two collections cited under this name by Räsänen (1932) has revealed that they are different species. One gathering from Martinez is fertile material of *U. aurantiaco-atra* and the other, from Yartou, is an infertile, immature specimen of *U. trachycarpa*. It is evident, from his notes on the herbarium packet, that Räsänen intended the fertile collection from Martinez to be the type of the variety since the presence of apothecia and spore measurements correspond with the published description.

Note 7: *Usnea siplei* Zammuto

This species was described from the Antarctic peninsula by Zammuto (*in* Dodge, 1965*b*), and, according to the description, the holotype is small and lacks apothecia and soredia. However, Dodge (1973) subsequently gave a similar description of the species but in the key describes it as being sorediate. A specimen, taken to be an isotype, bearing the same collection number (USAS 367, US!), and an additional collection (USAS 369, US!) from the same locality, both annotated *U. siplei*, have been examined. Both

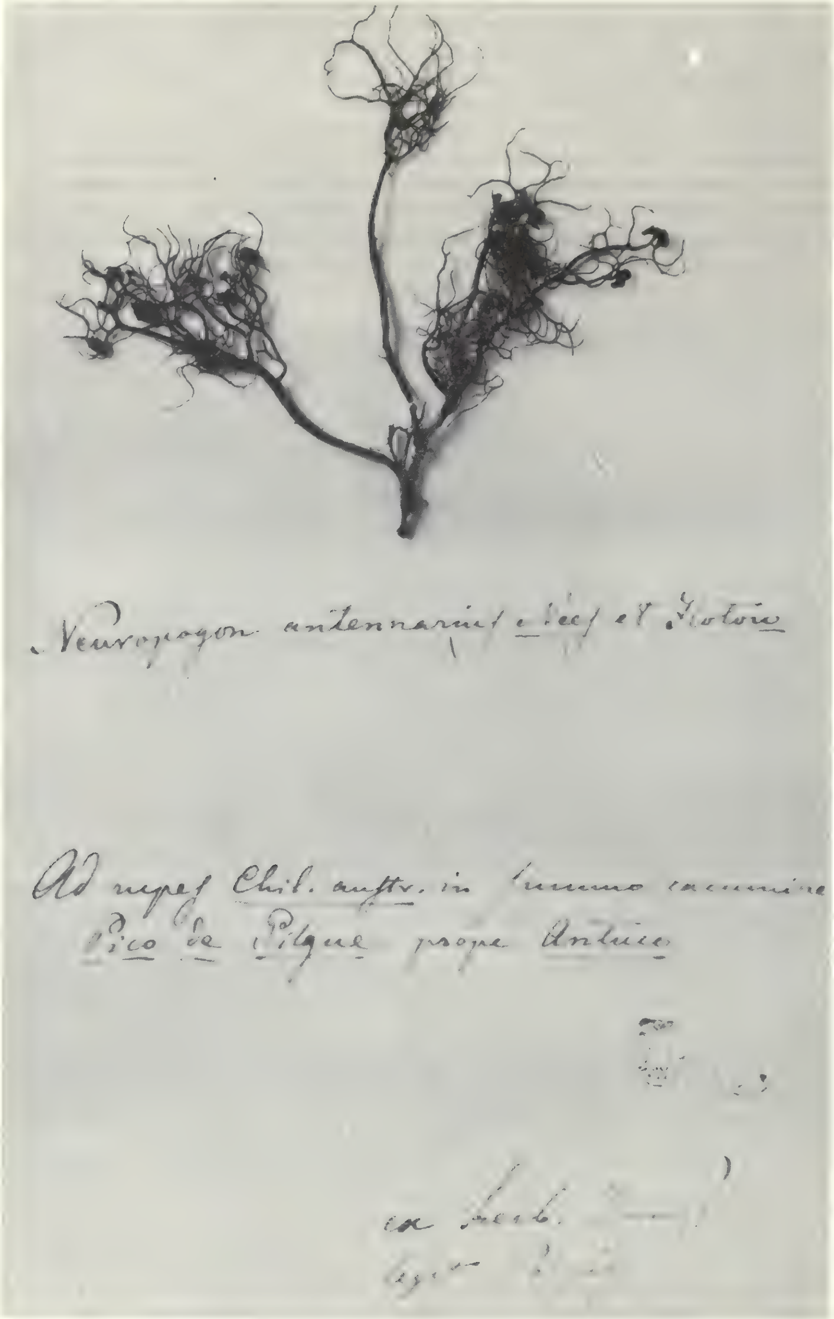

Neuropogon antennarius Nees et Flotow
Ad rupes Chil. austr. in summo cacumine
Pico de Pilque prope Antuco
ex herb.

Fig. 18 *Usnea aurantiaco-atra*. Lectotype of *Neuropogon antennarius* Nees & Flotow (VER) ×1.

are immature specimens of *U. aurantiaco-atra* as previously stated by Lamb (1948*a*). The isotype bears a single, small, immature apothecium. There is always the possibility that the original gathering may not have been homogeneous, and for this reason the species is only tentatively included here. Additional material from the Melchior Archipelago, collected by the same expedition, has been distributed as *Usnea fasciata* (Vězda: *Lich. Sel. Exs.* 675) and is moderately fertile.

Description: Thallus (3)–5–8(–10–13) cm, arising from a delimited or rarely proliferating ± pigmented holdfast, erect, ± dichotomous, richly branched above with numerous attenuate branches, fibrils rare. Branches terete or rarely angular, yellow-green, ± variegated above with bands of black to violaceous black pigment, ± continuously pigmented towards the apices. Cortex variable in thickness. Surface matt, ± smooth at base, becoming verrucose-rugose to subfaveolate-papillate, grossly papillate or ridged-faveolate above. Medulla compact, variable in extent, axis thick, occupying 0·5–0·6(–0·8) of the branch diameter. Soredia, pseudoisidia and isidia absent. Apothecia frequent, subterminal or rarely lateral, ± cupular, expanding on maturity. Disc black, excipulum verrucose-papillate, margin ± prominent, rays rare. Pycnidia infrequent towards branch apices. TLC: (1) fumarprotocetraric acid, ± protocetraric acid, ± cph-1, ± UV+ unknowns, usnic acid; (2) norstictic acid, salazinic acid, ± protocetraric acid, usnic acid; (3) no medullary substances, ± UV+ unknowns, usnic acid.

Distinguishing features: *Usnea aurantiaco-atra* is characterised by its erect habit, a richly branched thallus which is pigmented towards the apices, a verrucose to papillate surface, a compact medulla, a thick axis, and frequent subterminal apothecia with a black disc, usually lacking marginal excipular rays. It is the only fertile species of the subgenus which frequently contains fumarprotocetraric acid. (Fig. 16)

Distribution: *Usnea aurantiaco-atra* has a more restricted distribution than *U. antarctica* and is more or less confined to the west coast of the Antarctic peninsula, the islands of the Scotia Arc, including Bouvetøy, but excluding the South Sandwich Islands, and extends into subantarctic South America, including the Falkland Islands. The species does not occur in continental Antarctica (cf. Dalenius & Wilson, 1958) or Australasia. Specimens cited from Îles Kerguelen, collected by Hooker, are erroneously labelled, having been subsequently mixed with collections of *U. taylorii*. Fig. 4.

Chemistry: Three chemical races occur in *Usnea aurantiaco-atra*. Of these, specimens containing fumarprotocetraric acid (Race 1) and the depsidone deficient Race 3 are the most commonly encountered and have a much wider distribution than the norstictic-salazinic acid containing Race 2. Race 1 is apparently slightly more frequent than Race 2, with its centre of distribution in the South Orkneys and South Shetlands Islands; this race is also known from the Antarctic peninsula, South Georgia, Tierra del Fuego and Chile as far north as *c.* latitude 46°S. Race 3 extends further north, to *c.* 37°S, and further east to Bouvetøy, than Race 1.

Race 2 has its centre of distribution in the Falkland Islands, where Race 1 is only known from a few, possibly misplaced, collections. Race 2 overlaps Race 1 in southern South America, but is less frequent. It is confined to Tierra del Fuego apart from a single, isolated, northerly occurrence which forms the type specimen of *Neuropogon antennarius*: it is absent from the Antarctic peninsula. There are reports of occasional outliers of Race 2 from South Georgia (Lindsay, 1975) and rather tentatively from the South Shetlands (Motyka, 1936). Of these Lindsay's records were based on K and PD reactions which may have been misinterpreted since a high concentration of fumarprotocetraric acid can give a K+ red-brown reaction. In spite of these records, so far I have only confirmed (by TLC) two collections of Race 2 from South Georgia. Thalli of one gathering (*R. I. L. Smith* 259, AAS!) are extensively blackened and bear a superficial resemblance to *Usnea ciliata*, possibly due to the extremely exposed habitat given as a south-facing scree overlooking a glacier.

Very rarely thalli with a mixed chemical complement of Races 1 and 2 are encountered, particularly where the distributions of the two races overlap. For example, thalli may contain fumarprotocetraric, protocetraric, salazinic, and norstictic acids, or Race 1 may additionally contain salazinic acid, or Race 2 may either lack norstictic or salazinic acid and have a higher concentration of protocetraric acid. The implications of such thalli with mixed or intermediate chemistries are discussed under 'species concept' below.

Variation: *Usnea aurantiaco-atra* is a very variable, but usually easily recognised species, even when sterile. It exhibits a wide range of growth form, branch anatomy, and degree of pigmentation. The account of *U. antarctica* (p. 58) should be referred to for discussion of much of the variation in branching, morphology, and anatomy. Thalli may rarely become subdecumbent or straggling and then may be sparsely pigmented, sterile, and infrequently to richly branched; such specimens superficially resemble *U. neuropogonoides*. In rare instances pigment may be confined to branch apices and the apothecial disc, which seem to be more prevalent in Race 2.

In contrast to *Usnea antarctica* thalli are often larger, though rarely more than 10 cm. In *U. aurantiaco-atra* a wider range of variation is found in surface ornamentation and branch anatomy, which, although frequently correlated with medullary chemistry, is not sufficiently distinct to merit taxonomic separation. For example, the lectotype of *Lichen aurantiaco-ater*, typical of Races 1 and 3, is minutely verrucose-papillate and is extensively branched with continuously pigmented ultimate branches. The axis occupies more than half the branch diameter and in transverse section branches are more or less terete and have a narrow medulla, *c.* 200 μm. In contrast, the type of *Usnea melaxantha*, typical of Race 2, has branches which are somewhat angular-indented in section resulting from faveolation and deeper depressions. The axis of *U. melaxantha* is somewhat irregular in outline and occupies slightly less than half the diameter coupled with a correspondingly wider medulla of up to 300 μm.

Ornamentation ranges from almost smooth to obscurely papillate to coarsely verrucose-papillate becoming distinctly faveolate-ridged. False annulations, resembling those of *Usnea ciliata*, only occur in exceptionally smooth, scantily papillate or weakly verrucose thalli that have been extensively weathered, for example, as in the types of *U. trachycarpa* var. *eciliata* and *Neuropogon antennarius*. On occasions a range of ornamentation may be exhibited by a single thallus. Fibrils are only rarely produced as extended papillae or verruculae and are never as extensively developed as those of *U. trachycarpa*. Fibrillate forms previously given taxonomic status include *N. melaxanthus* var. *fibrillifer* and *U. melaxantha* var. *nigropallida*; one taxon, *U. melaxantha* var. *subciliata* f. *strigulosa*, was even raised to specific rank (Lamb, 1939*a*; Motyka, 1936).

The axis may be somewhat irregular in outline and can vary in thickness together with the width of the medulla, which tends to be broader in Race 2. Overall it is rare for the axis to occupy more than 0·7 of the branch diameter. Exceptions include the type of *Usnea taylorii* var. *kranckii*, which is here treated as a synonym, as well as specimens examined from Bouvetøy (BG!); in these the axis occupies 0·7 to 0·8 of the branch diameter and the medulla is narrowed to *c.* 100 μm in primary branches, suggesting a possible affinity with *U. taylorii*.

Apothecia are normally subterminal, rarely with a geniculate appendage, or may be lateral. In some instances the margin may become excluded and the apothecium irregular and reflexed, or even slightly crenulate in well-developed thalli. Only rarely is the disc pigmentation not fully developed (for example, *R. I. L. Smith* 2573, AAS!). The excipulum is papillate or minutely faveolate; irregular rays are only rarely produced and then in thalli which develop fibrils on main branches.

Species concept: To date various taxa comprising the *Usnea aurantiaco-atra–U. melaxantha* group have been considered to be distinct species by different authors (Table 4). Dodge (1973) recognised six species, Motyka (1936) five; Lamb initially (Lamb, 1939*a*) accepted four species but finally modified his concept to include only two (Lamb, 1964). Apart from the ensuing nomenclatural confusion the delimitation of each species was by no means clear and depended on small variations in the relative size of axis and medulla, surface ornamentation or presence of fibrils, thallus size or the extent of branching. Variation in chemical reactions was also considered to be significant; for example the depsidone-deficient *Neuropogon aurantiaco-ater* f. *egentissimus* as well as *Usnea sulphurea* var. *normalis* f. *activa* which gave an intense K+ red reaction.

Motyka (1936) considered that the species could be separated primarily on morphological features, but Lamb later (Lamb, 1948*a*) considered chemistry to be the only reliable feature and used thallus spot tests to distinguish *Usnea melaxantha* from *U. aurantiaco-atra* (i.e. Races 1 and 3 from Race 2). Lindsay, (1975) used chemistry initially to distinguish between the two taxa, but included differences in surface ornamentation in his descriptions. Eventually Lamb (1964) concluded that there were morphological and distributional differences between the two species which were supported by chemistry. These differences, however, were only apparent when contrasting whole populations rather than considering individuals. This approach is, however, in my estimation impractical, as admitted by Lamb (1964), since many thalli with intermediate characters may occur, particularly where the distributions of chemical races overlap. This leaves chemistry as apparently the only reliable criterion for separating *U. aurantiaco-atra* from *U. melaxantha*. These two taxa are here considered to form chemical races of a single species particularly as all the substances involved have a close biosynthetic relationship (Huovinen & Ahti, 1982).

During this investigation it has been found that even chemistry may not, on very rare occasions, be sufficiently reliable to separate '*melaxantha*' and '*aurantiaco-atra*' type thalli. TLC studies indicate that chemical data are not always correlated with minute morphological differences. Morphological similarities between the two chemical races are particularly apparent in material from the Magellan Straits area, where Races 1 and 2 overlap at the western limit of Race 2 and both races are often collected together. In particular Menzies' collections of 1787 from Isla de los Estados (Staten Island) include a diverse range of chemistries in an apparently morphologically and anatomically uniform gathering. These collections were widely distributed throughout herbaria and represent paratype material of *Usnea melaxantha* (BM, E, H (ACH), LINN, PC, UPS, US). Out of 32 thalli examined by TLC one plant was depsidone deficient, 20 belonged to Race 1 and 11 to Race 2 although often lacking either norstictic or salazinic acid, but sometimes with traces of protocetraric acid. A further specimen from the same area (*Castellanos* 1542, BM!) only contained salazinic acid. Other examples of specimens with a mixed chemistry include a collection from Ushuaia (*Henssen & Vobis* 24 417a, MB!) in which two thalli contained salazinic acid in addition to the substances of Race 1, and a specimen from the Falkland Islands (*R. I. L. Smith* 2572, AAS!) which contained norstictic, salazinic, fumarprotocetraric and protocetraric acids.

Examination of transverse sections from main branches of thalli in one of the Menzies collections (E), Fig. 19, representing both chemical races, are identical, with the axis occupying approximately half the branch diameter and with cortex and medulla widths 70–75 μm and 170–200 μm respectively. An additional specimen from Isla de los Estados (H36372!) has a somewhat wider medulla and is more angular in transverse section and is characteristic of the so-called '*melaxantha*' form. However, this thallus contains fumarprotocetraric acid (Race 1) instead of norstictic acid (Race 2). Surface ornamentation is frequently not so distinct in some of these specimens; there is a tendency in both races for the thallus to be smoother with less pronounced ornamentation, particularly towards the base, to occasionally become subnitid, but only rarely rupture to form annulations. Typically, fumarprotocetraric acid containing specimens (Race 1) have been described as being verrucose-papillate, rarely becoming scrobiculate-corrugated, whilst norstictic and salazinic acid containing specimens are described as being sparsely papillate becoming confluent and scrobiculate-corrugated (Lindsay, 1975). However, all these states are frequently found on the same thallus and are probably associated with its age and the degree of exposure. Slight difference in thallus colour has also led to the recognition of separate taxa that are here regarded as synonyms; for example *Cornicularia flavicans*. Likewise Motyka (1936) distinguished *Usnea melaxantha* from other taxa on the width and pinkish colour of the medulla, a feature that was subsequently found to be a storage artefact involving the breakdown of salazinic acid.

Usnea aurantiaco-atra has most frequently been confused with *U. ciliata* and *U. perpusilla*. Apart from differences in distribution the species may be distinguished from *U. ciliata* by the ornamented surface, which lacks a waxy lustre and the typical pigmented annulations, and the frequent absence of excipular rays. The medulla of *U. aurantiaco-atra* is more compact than is usually found in *U. perpusilla* and the apothecia are frequently subterminal (Fig. 2) rather than lateral in series. The species may be distinguished from *U. trachycarpa* by differences in disc colour, abundance of fibrils and width of the medulla; and from *U. taylorii* by the latter's unique anatomy.

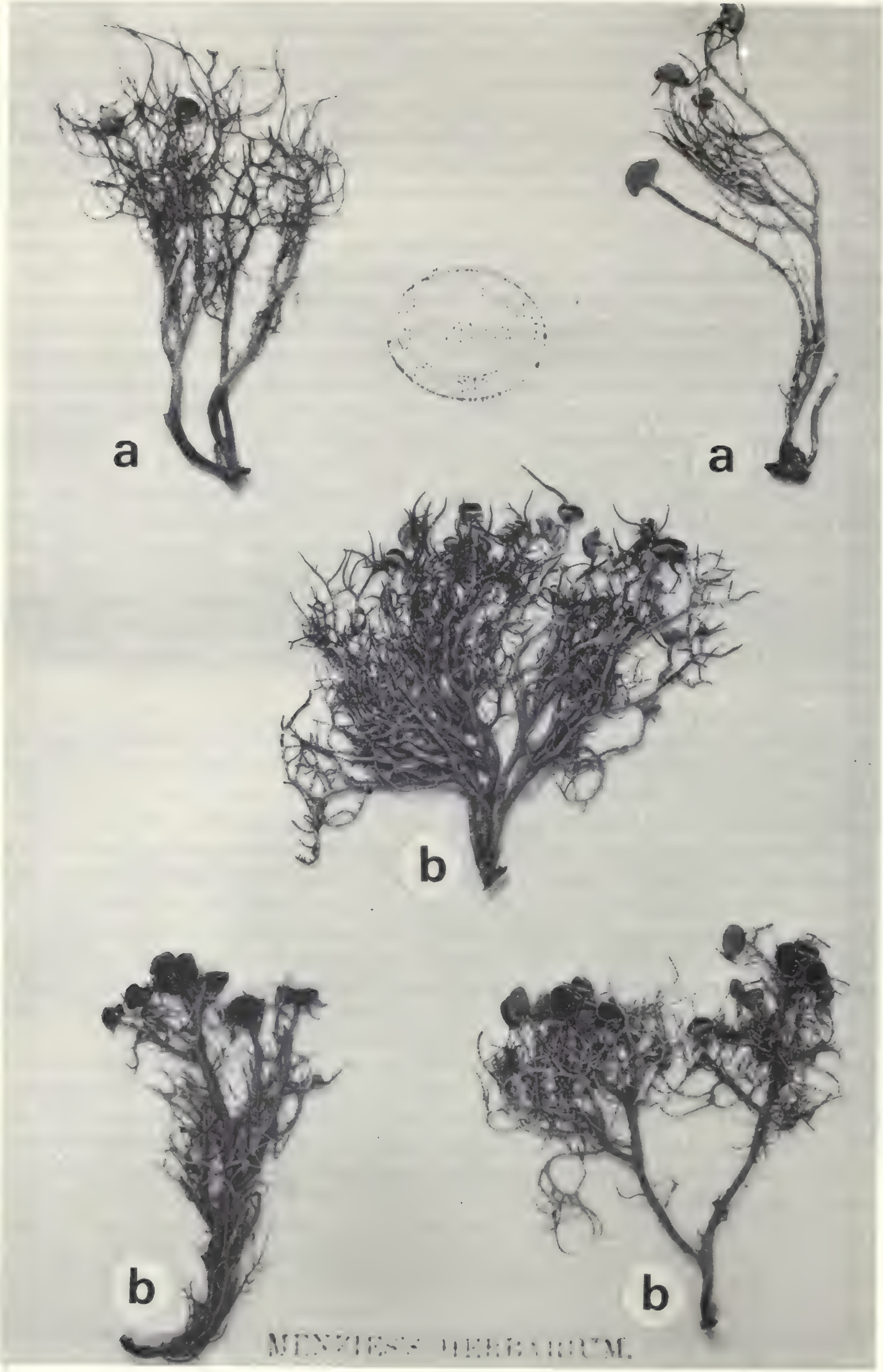

a
a
b
b
b
MENZIES'S HERBARIUM.

Fig. 19 *Usnea aurantiaco-atra.* a = Race 1, b = Race 2. Staten Land, February 1787, *Menzies* (E) ×1.

Selected specimens examined

Race 1

CHILE. Aisén: Coyhaique, Cerros Divisaderos (Cordon de Bella Vista), 1300 m, 13 November 1940, *R. Santesson* 6843 (S), 1400 m, 13 November 1940, *R. Santesson* 7355 (CANL 16965, S). Magallanes: Punta Arenas, Cerros Mina Rica, *c.* 500 m, 22 December 1940, *R. Santesson* 5244 (S, UPS); Tierra del Fuego, Porvenir, Morro Piedra, 300 m, 30 December 1940, *R. Santesson* 5398 (S); Isla Navarino, Puerto Navarino, 10 m, 28 February 1940, *R. Santesson* 1233 a & b (S); Cabo de Hornos, Hermite I., Forster's Peak, 1842, *R. McCormick* s.n. (BM); Tierra del Fuego, Canal Whiteside, Nose Peak, *R. Santesson* 5965, Lich. austram. ex Herb. Regnelliano 422 (BM, C, H, S, UPS).

ARGENTINA. Chubut: Comodoro Rivadavia, 1924 '*Euero*' 22 (BM). Tierra del Fuego: Sierra Alvear, S. slope, above Las Cotorras (*c.* 20 km ENE. of Ushuaia), 800–900 m, 7 February 1940, *R. Santesson* 639a (S, UPS); Montes Martiales, above Ushuaia, 10 March 1965, *I. M. Lamb* 8146 (FH, M); Beagle Channel, February 1963, *E. E. Shipton* s.n. (BM); Isla de los Estados, February 1787, *A. Menzies* s.n. [+ Races 2 & 3] (BM, E, H (ACH), LINN, PC, UPS, US).

SOUTH GEORGIA. Cumberland West Bay, 2 km N. of Mt. Hodges, 28 February 1972, *D. C. Lindsay* 4285 (AAS, BM); Cumberland West Bay, near head of Sphagnum Valley, *c.* 150 m, 1 February 1961, *S. W. Greene* 1617 (AAS); Grytviken, 25 December 1909, *C. A. Larsen* s.n. (O, UPS).

SOUTH ORKNEY IS. Signy I.: Factory Bluff, NE., 19 January 1965, *J. Price* 9 (BM); Observation Bluff, 107 m, 6 February 1966, *D. C. Lindsay* 867 (AAS). Coronation I.: Foot of Wave Peak Buttress, Marshall Piedmark, 210 m, 20 August 1950, *W. J. L. Sladen* F.I.D.S. H602/3 (BM); Olivine Point, 30–60 m, 17 January 1965, *R. I. L. Smith* 156 (AAS, BM, FH). Laurie I.: Cape Geddes, 15–60 m, 13 February 1971, M. *McManmon* 140 (AAS).

SOUTH SHETLAND IS. King George I.: Admiralty Bay, Keller Peninsula, Mt. Flagstaff, 265 m, 9 January 1980, *R. Ochyra* 416/80 (M); Fildes Peninsula, 168 m, 16 February 1966, *B. S. John & D. E. Sugden* 25 (AAS, BM). Livingston I.: Robbery Beaches, Byers Peninsula, 75 m, 30 December 1965, *D. C. Lindsay* 518 (AAS). Half Moon I.: 75 m, 5 January 1966, *D. C. Lindsay* 576 (AAS, BM, FH). Robert I.: English Strait, Copper Mine Cove, *c.* 60 m, 31 December 1934, *'Discovery' Exped.* 14851 (BM).

ANTARCTIC PENINSULA. Graham Land: Joinville I. [63°15'S: 55°45'W], Mt. Alexander, 200–500 m, 27 March 1981, *R. I. L. Smith* 3680 p.p. (AAS); Palmer Archipelago, Melchior Is., Omega [Lystad] I. [64°20'S: 62°56'W], 28 January 1951, *A. Martínez* s.n. (FH), 6–9 m, 14 March 1941, *P. A. Siple* U.S.A.S. 369 (US), Anvers I. [64°45'S: 64°05'W], Arthur Harbour, 20 m, 6 February 1965, *I. M. Lamb & M. Zimmerman* 8091 (FH), Wiencke I. [64°48'S: 63°25'W], N. buttress of Noble Peak, 225 m, 20 November 1944, *I. M. Lamb* Operation Tabarin 1790 p.p. (BM), *I. M. Lamb* Operation Tabarin 1789 (BM, CANL 16961, FH); Argentine Is., Galindez I. [65°15'S: 64°15'W], Woozle Hill, 35–50 m, 5 March 1981, *R. I. L. Smith* 3304 (AAS), summit, 1 January 1936, *B.G.L.E.* 1340 p.p. (BM, FH), Uruguay I. [65°14'S: 64°14'W], 15 m, 25 October 1964, *R. W. M. Corner* 603 (AAS); Graham Coast, near Cape Tuxen [67°44'S: 68°25'W], 26 January 1961, *K. Archibald* 33 (AAS).

Race 2

CHILE. Bío Bío: Type of *Neuropogon antennarius* (VER). Magallanes: Tierra del Fuego, Canal Whiteside, Puerto Yartou, Nose Peak, 700 m, 5 February 1941, *R. Santesson* 6820 (S); Cabo de Hornos, Hermite I., 1839–43, *J. D. Hooker* s.n. (BM, E); Magellan Straits, Cerros Yartou, 8 March 1928, herb. Th. Fries (UPS).

ARGENTINA. Tierra del Fuego: Cerro Garibaldi, SE. of Lago Escondido, between Ushuaia and Rio Grande, 1961, *R. M. Schuster* 58346 p.p. (CHR 342819, FH); Isla Navarino, Puerto Navarino, 10 m, 28 February 1940, *R. Santesson* 1232c (S); Canal Beagle, W. of Lapataia Bay, 1898, *M. E. G. Racovitza* 188 p.p. (herb. Vain. 344 – TUR 458).

FALKLAND IS. East Falkland I.: Stanley, Sapper Hill, 4 April 1965, *J. Price* s.n. (BM), Stanley, 30 January 1946, *I. M. Lamb* Vězda: Lich. Sel. Exs. 496 (BM, M, MB); Mt William, near Stanley, near sea-level, 30 January 1946, *I. M. Lamb* Operation Tabarin 2891 (CANL 17185), Operation Tabarin 2888 (BM); Mt. Longdon, 174 m, 2 April 1967, *D. C. Lindsay* 1659 (AAS, H); between Darwin and Goose Green, 6 m, 17 September 1963, *R. W. M. Corner* 53 (AAS, FH); N. of Wireless Hill, 100 m, 28 February 1977, *R. I. L. Smith* 2574 (AAS). West Falkland Is.: Roy Cove, 1909–11, *E. Vallentin* 88 (BM).

SOUTH GEORGIA. *c.* 1 km SE. of Brocken, 180 m, 23 January 1972, *D. C. Lindsay* 4036 (AAS); E. of Swinhoe Peak, between Hamburg Lakes and Hamburg Glacier, 690–695 m, 6 November 1976, *R. I. L. Smith* 2519 (AAS).

Race 3

CHILE. Bío Bío: Antuco, *Reynolds* 141 (BM). Cautín: Andes de Villarrica, 1891, *Neyer* s.n. (M). Magallanes: Cape Spencer, *J. D. Hooker* s.n. (E); Cabo de Hornos, Hermite I., St. Martin's Cove, *R.*

McCormick s.n. (BM); Cabo de Hornos, Voyage of H.M.S. *Adventure* and *Beagle* 1826–30, *King* s.n. (BM).
ARGENTINA. Neuquén: Parque Nacional Lanín, N. of Lago Lacar, Cerro Malo, *c.* 1900 m, 28 January 1968, *J. H. de Haas* 1290 (U 313673b). Río Negro: Cerro Rigi, near Lago Frias, *c.* 1780 m, 15 February 1950, *I. M. Lamb* 6045 (CANL 16962, UPS), 1660 m, *I. M. Lamb* 6043 (CANL 16964, FH, H, US). Tierra del Fuego: Fuegia med., Cerro Milladeo, 850 m, 17 January 1929, *H. Roivainen* s.n. (H).

SOUTH GEORGIA. Head of Sphagnum Valley, near Echo Pass, Cumberland West Bay, 15 January 1961, *E. A. Coleman* Greene 1071 (AAS, BM, FH); Wilson Harbour, 19 January 1927, *'Discovery' Exped.* s.n. (BM).
SOUTH ORKNEY IS. Signy I.: Hill between Factory Cove and Paal Harbour, 105 m, 20 December 1961, *M. W. Holdgate* 225 (AAS). Coronation I.: Saunders Point, 0–9 m, 8 October 1950, *W. J. L. Sladen* F.I.D.S. H 612/21 (BM).
SOUTH SHETLAND IS. King George I.: Keller Range, 21 February 1947, *D. Nicholson & A. Reece* Vězda: Lich. Sel. Exs. 972 (BM). Livingston I.: New Plymouth, Byers Peninsula, 19 m, 14 December 1965, *D. C. Lindsay* 366 (AAS). Nelson I.: Harmony Cove, 2 December 1954, *O. Kühnemann* 35075 (FH).
ANTARCTIC PENINSULA. Graham Land: Joinville I. [63°15′S: 55°45′W], Mt. Alexander, 250 m, 27 March 1981, *R. I. L. Smith* 3682 (AAS); Palmer Archipelago, Wiencke I. [64°48′S: 63°25′W], N. buttress of Noble Peak, 225 m, 20 November 1944, *I. M. Lamb* Operation Tabarin 1789 (BM); Argentine Is., Galindez I. [65°15′S: 64°15′W], above Stella Creek, 24 m, 21 April 1964, *R. W. M. Corner* 542 (BM), Corner I. [65°16′S: 64°14′S], 6 m, 18 August 1964, *R. W. M. Corner* 566 (AAS), Graham Coast, Loubat Point [65°04′S: 63°56′W], Lemaire Channel, 300 m, 19 March 1964, *J. Clennell* Kennett 56 (AAS, BM).
BOUVETØY. Rustadkollen SW., 323 m, 7 March 1979, *T. Engelskjøn* s.n. (BG, BM).
Races 1 + 2
(see p. 71)
ARGENTINA. Tierra del Fuego: Parque Nacional Tierra del Fuego, 'Weg zum' Glaciar Martial, *c.* 500 m, 7 December 1973, *A. Henssen & G. Vobis* 24 417a (MB).
FALKLAND IS. East Falkland I.: to N. of Wireless Hill, 28 February 1977, *R. I. L. Smith* 2572 (AAS).

The following may be consulted for further localities: South America (Lamb, 1948*a*), South Georgia (Lindsay, 1975), South Orkney Is. (Smith, 1973), South Shetland Is. (Lindsay, 1971*a*), Antarctic Peninsula (Lamb, 1964); together with lists held in BM and collections in AAS and BM.

5. **Usnea ciliata** (Nyl.) Du Rietz **Figs 20–21**

in *Svensk. bot. Tidskr.* **20**: 91 (1926). – *Neuropogon melaxanthus* var. *ciliatus* Nyl. in *J. Linn. Soc.* (Bot.) **9**: 245 (1866). – *Neuropogon ciliatus* (Nyl.) Krempelh. in *Ver. zool.-bot. Ges. Wien.* **18**: 313 (1868). – *Usnea melaxantha* var. *ciliata* (Nyl.) Müll. Arg. in *Bull. Soc. r. Bot. Belg.* **31**(2): 26 (1892). Type: New Zealand, Tarndale, Nelson Mountains, January 1861, *Dr A. Sinclair.* (H-NYL 36365! – holotype; BM!, E! – isotypes). [TLC: norstictic acid, salazinic acid, ± protocetraric acid, usnic acid.]

Note: The combination *Usnea ciliata* (Müll. Arg.) Vainio (Vainio, 1909) was invalidly published in synonymy (Article 34.1) and consequently does not predate the name *U. ciliata* (Nyl.) Du Rietz. Further, Vainio, in later publications (Vainio, 1913, 1915, 1923), made it clear that he intended the name to be published as *U. trichoidea* * *U. ciliata*, thus making a combination below specific rank.

Description: Thallus (–3)–5–10(–12) cm, arising from a broadly proliferating, pigmented holdfast, erect, ± monopodial or subdichotomous, moderately branched above, fibrils absent, lacking extended secondary branches. Branches terete, yellow-green, ± continuously pigmented violaceous black towards the apices. Cortex thick. Surface smooth, or rarely subfaveolate, waxy, epapillate, with conspicuous black-edged annulations. Medulla compact, axis thick, occupying *c.* 0·5 of the branch diameter. Soredia, pseudoisidia and isidia absent. Apothecia frequent, subterminal, geniculate with a subtending spur, or additionally lateral; cupular or plane becoming reflexed on maturity. Disc black, ± excluded margin, excipulum smooth or subfaveolate, marginal rays ± limited in number, stout, branch-like, pigmented. Pycnidia not seen. TLC: norstictic acid, salazinic acid, ± protocetraric acid, usnic acid.

Distinguishing features: Usnea ciliata is characterised by its erect habit, arising from a proliferating holdfast, and a monopodial to moderately branched thallus, often with violaceous black pigmentation, a smooth, waxy, black-annulate surface, a compact medulla containing

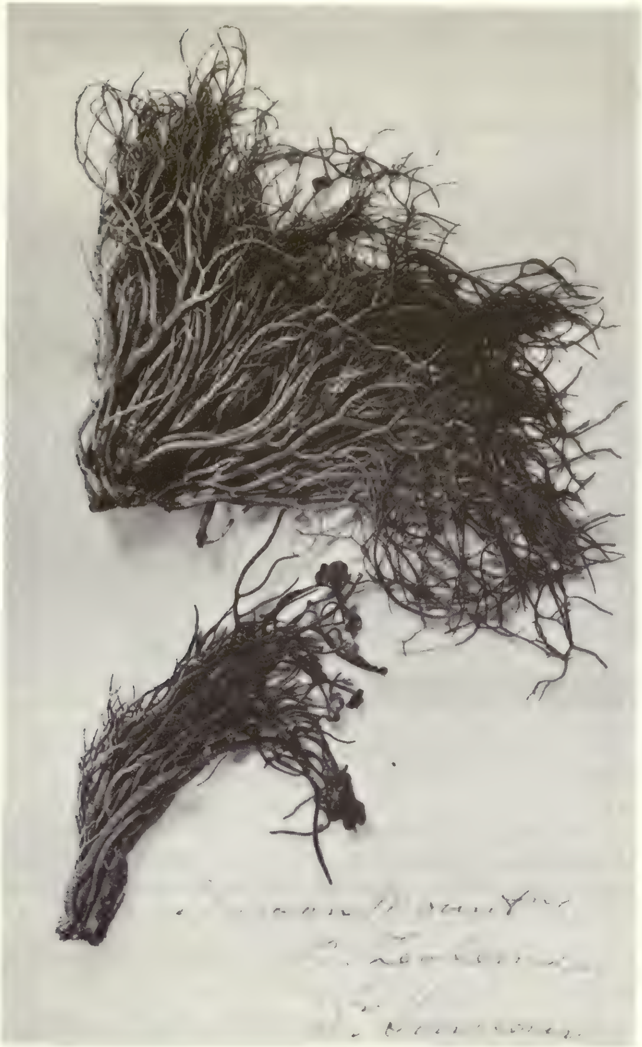


Fig. 20 *Usnea ciliata*. Isotype of *Usnea melaxantha* var. *ciliata* Nyl. (BM) ×1.

norstictic and salazinic acids, a thick axis, and subterminal, geniculate apothecia with a black disc and conspicuous excipular rays.

Distribution: *Usnea ciliata* is confined to Australasia and is only known with certainty from New Zealand, where it has a similar, but slightly more restricted distribution, to *U. acromelana*, often absent at lower altitudes. Its presence in the North Island has now been confirmed by recent collections made by Bartlett (p. 22), although the species is undoubtedly rare and less frequently fertile there; occasionally *Alectoria nigricans* has been mistaken for such sterile thalli (for example, Mt. Ruahine, *Colenso* 1164A WELT!). The species is also rare on Stewart Island. Tasmanian records remain uncertain and are either based on damaged material lacking either apothecia or soredia (for example, *Bratt,* CHR342744!), or have not been traced (for example, Dodge, 1948). However, it is possible that *U. ciliata* does rarely occur in Tasmania, although this cannot be verified in the absence of fertile material.

Lamb (1939*a*, 1948*a*, 1959) cited several collections of *Usnea ciliata* from South America. Many of these have been examined and are less typical, almost smooth, forms of either *Usnea*

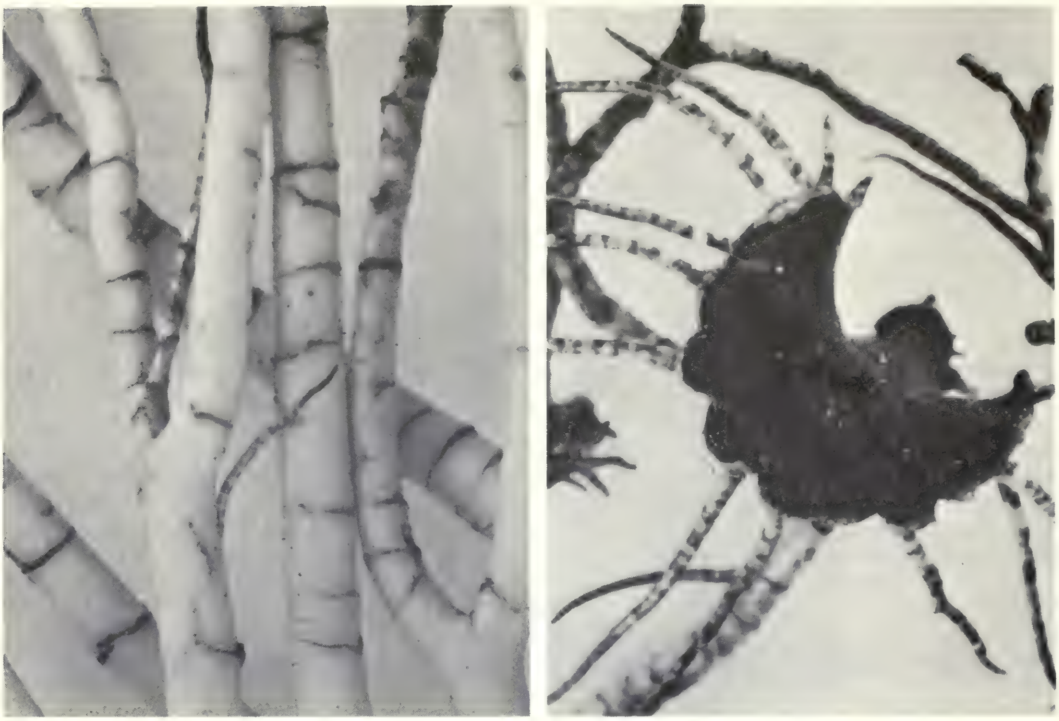


Fig. 21 *Usnea ciliata*. New Zealand, Otago, Rock & Pillar Range, February 1967, *Galloway* (BM). Left. Detail of cortical annulations ×10. Right. Detail of apothecium ×10.

aurantiaco-atra or, alternatively, *U. perpusilla*, in which the medulla is not characteristically lax. In both instances the apothecia bear some excipular rays and any annulations present are of a spurious nature, merely the result of weathering. The specimen figured by Lamb (1939*a* pl. 7 fig. 13, herb. Vainio 344 TUR 458!) is *U. aurantiaco-atra* (Race 2). Fig. 6.

Chemistry: To date only one chemical race, that containing norstictic and salazinic acids, is known from the large number of collections examined.

Variation: *Usnea acromelana* should be referred to (p. 50) for the account of variation in branching, pigmentation, morphology and anatomy, which may, to a similar extent, be influenced by altitude. However, *U. ciliata* does not exhibit such a wide range of variation as *U. acromelana*.

The degree of violaceous black pigmentation is often extensive in more richly branched forms, but in extreme instances it may only be present in the apothecial disc, annulations and branch and ray apices. The thalli are often taller than those of *Usnea acromelana* and tend to show less variation in the proliferating nature of the holdfast. Small, tufted, densely branched forms, with fine, tapering secondary branches may be distinguished from *U. subcapillaris* by their erect habit and shorter, stouter branches (see p. 106).

Apothecia are usually subterminal and conspicuously geniculate with a subtending spur that may be longer than the excipular rays. Additional, lateral, apothecia may sometimes be produced which tend to be subsessile. Their size is variable, as is the presence, number, length, and occasional branching, of excipular rays, which are not as extensively produced as in *Usnea trachycarpa*. Young apothecia are cupular, becoming expanded or sometimes convex at maturity, when they are irregular to crenulate. Only in rare instances is the black pigmentation of the disc more or less lacking or not fully developed. The excipulum is usually smooth but may sometimes be subfaveolate, thus reflecting the subtending branch morphology; the margin is often excluded.

Species concept: *Usnea ciliata* is a comparatively uniform species which is considered to be the primary species related to the sorediate *U. acromelana*. Although it is closely allied to *U. subcapillaris*, only in very rare instances are thalli encountered that appear to be intermediate between the two taxa. *U. ciliata* may be distinguished from *U. subcapillaris* by its erect rather than subdecumbent habit, the coarser, shorter secondary branches, and subterminal, rather than lateral, apothecia.

Usnea ciliata may be separated from other fertile species by distribution, although it is readily distinguishable on morphological characters.

Selected specimens examined

NEW ZEALAND. North Island. Gisborne: Mt. Hikurangi, *c.* 1740 m, 14 November 1983, *J. K. Bartlett* 25965 (BM). Hawke's Bay: Mt. Kaweka, *c.* 1840 m, 9 November 1983, *J. K. Bartlett* 25960 (BM), *J. K. Bartlett* 25961 (BM). Wellington; Mt. Ruapehu, Turoa Site, 1740 m, 6 July 1969, *D. J. Galloway* s.n. (CHR 342790, CHR 343281, CHR 343292, CHR 343339); near Wellington [? Tararua Range], *J. Buchanan* s.n. (BM, GLAM NHB 1927-8-347); North Ruahine Range, *c.* 1000 m, 17 October 1983, *J. K. Bartlett* 26688 (herb. Bartlett).

South Island. Nelson: Mt. Cobb, *c.* 1740 m, 19 December 1982, *J. K. Bartlett* 24724a (herb. Bartlett, BM); near Dunn Saddle, 1460 m, 12 January 1983, *J. K. Bartlett* 25962 (BM); Kakapo Peak, *c.* 1520 m, 16 December 1982, *J. K. Bartlett* 26253 (herb. Bartlett, BM), *J. K. Bartlett* 25812 (herb. Bartlett, BM); Mt. Robert, Lake Rotoiti, 1430 m, 16 January 1960, *D. Scott* 426 (BM); St. Arnaud Range, 1680 m, 22 December 1967, *A. F. Mark* s.n. (CHR 343290 p.p., CHR 343321); Mt. Technical, above Lewis Pass, 14 January 1979, *D. J. Galloway* s.n. (CHR 343160 p.p.); Mt. Aorere, *J. K. Bartlett* s.n. (CHR 343235); Lake Sylvester, 1620 m, 18 December 1967, *A. F. Mark* s.n. (CHR 342797, CHR 342798). Marlborough: Mt. Black Birch, 1220 m, 1 January 1969, *B. V. Sneddon* s.n. (BM, CHR 342822); Blue Mtn, near head of Waihopai River, *c.* 1830 m, 1934, *W. Martin* s.n. (CHR 375942); Upper Awatere Valley, Shingle Peak, 1310 m, 6 January 1970, *A. F. Mark* s.n. (OTA 27124); Awatere, Mt. Harkness (collector unknown) (CHR 160678); Inland Kaikoura Range, Mt. Tapuaenuku, 20 March 1934, *J. S. Thomson* 1523 p.p. (CHR 343806 p.p.), 2700 m, August 1969, *P. Lusk* s.n. (CHR 343309), February 1961, *B. C. Aston* s.n. (WELT L193), 1859, *Sinclair* s.n. (BM); Inland Kaikoura Range, Mt. Mitre, 27 January 1954, *R. Mason & D. R. McQueen* s.n. (CHR 160686 p.p.); Upcot, February 1916, *B. C. Aston* s.n. (WELT L190). Canterbury: Torlesse Range, Foggy Peak, 1680 m, 18 December 1962, *P. W. James* 1918 p.p. (BM), 12 November 1972, *G. C. Bratt* 72/1880c (HO 35166); Mt. Torlesse, March 1934, *J. S. Thomson* 1618 (CHR 343800); Four Peaks Range, Blue Mountain, *c.* 1640 m, 23 April 1979, *D. J. Galloway* s.n. (CHR 343225); Mt. Peel, 1740 m, January 1972, *D. J. Galloway* s.n. (BM, CHR 343437), *c.* 1680 m, *H. H. Allan* 2 (UPS); Mt. Peel, Rangitata River, 1520 m, 6 May 1960, *D. Scott* 458 (OTA); Kirkliston Range, 1680–1830 m, 25 March 1978, *D. J. Galloway* s.n. (CHR 343254); Two Thumb Range, Mt. Richmond, November 1968, *A. F. Mark* s.n. (CHR 343302); Two Thumb Range, Mt. Dobson, 1830 m, 15 January 1959, *D. Scott* 302 (OTA); Craigieburn Range, 1520 m, October 1968, *L. J. W. Strang* s.n. (CHR 342783); Temple Basin, Arthur's Pass, 21 February 1943, *V. D. Zotov* s.n. (CHR 160683); Cass, Day Creek, 1070 m, 6 February 1936, *M. Sutherland* s.n. (WELT L194); Ben Ohau Range, Glen Lyon Station, 1830 m, October 1958, *Mason* 161 & 162 (OTA); Porter's Pass, February 1874, 910 m, *S. Berggren* s.n. (UPS); Banks Peninsula, Castle Rock, 460 m, October 1967, *P. F. Johnson* s.n. (CHR 342785). Otago: Rock and Pillar Range, 1160–1190 m, 18 September 1981, *F. J. Walker* s.n. (BM, UPS), *c.* 1020 m, 4 April 1970, *G. Degelius* NZ-346 (herb. Degelius), 2000 m, 1 December 1969, *N. M. Adams* s.n. (WELT L359); Old Man Range, 1370 m, 1 February 1963, *P. W. James* 1576 (BM), 1680 m, April 1968, *D. J. Galloway* s.n. (BM, CHR 343341); Mt. Sir William, 2560 m, 27 December 1970, *D. J. Galloway* s.n. (CHR 34278 p.p.); Humboldt Mtns, Mt. Nox, 1950 m, 31 December 1969, *D. J. Galloway* s.n. (CHR 342791 p.p.); Remarkables, 1220 m, February 1968, *D. J. Galloway* s.n. (CHR 343334); Matukituki Valley, Mt. Avalanche, 1680 m, 5 April 1969, *L. D. Kennedy* s.n. (CHR 342756); Mt. Maungatua, 910 m, March 1954, *J. Murray* 554 (OTA); Lake Ohau, Mt. Sutton, 1070 m, May 1958, *J. Murray* 1783 (BM); Mt. Roy, 1 November 1972, *G. C. Bratt* 72/1507 (HO 35174); Mt. Pisa, 1860 m, March 1968, *D. J. Galloway* s.n. (CHR 342799); Silverpeaks, Gap Ridge, 610 m, 19 March 1961, *D. J. Galloway* s.n. (CHR 342754). Southland: Mid Dome, 1520 m, May 1970, *G. Van Reenen* s.n. (CHR 342837 p.p.); West Dome, 1070 m, 11 January 1970, *P. N. Holdsworth* s.n. (CHR 342806); Ridge between Takahe Valley and Ettrick Burn, 1400 m, 16 February 1969, *G. Van Reenen* s.n. (CHR 342818); Thomson Mtns, 1370 m, October 1967, *A. F. Mark* s.n. (CHR 342813); Grave-Talbot Pass, Milford Track, 1830 m, 25 January 1963, *O. Fletcher* s.n. (CHR 160684). Stewart I.: Mt. Anglem, 992 m, February 1966, *D. J. Galloway* s.n. (CHR 342749).

For further localities in Canterbury and Otago see lists held in BM and collections in CHR, HO and OTA.

6. Usnea durietzii Motyka **Fig. 22**

Lich. Gen. Usn. Stud. Monogr. **2**: 503 (1937). Type: [Chile] *W. Lechler: Plantae Magellanicum*, Insula Elizabethae [54°07′S: 73°11′W] Oct. med. 1882 (UPS! – holotype; BM!, M!, PC! – isotypes). [TLC: norstictic acid, salazinic acid, usnic acid.]

Description: Thallus 2–3(–4) cm, arising from a single, ± elongated, blackened holdfast, erect, richly branched, often 0·5–1·0 cm above the base, main branches clustered, fibrils absent, with short, recurved, capillaceous secondary branches. Branches terete, greenish yellow, ± articulate, conspicuously inflated above a ± constricted base, black-pigmented only at the apices. Cortex thin. Surface matt, coriaceous, usually epapillate. Medulla broad, very lax in main branches, axis thin, occupying 0·2–0·4 of the branch diameter. Pseudoisidia numerous on all branches, in soralia-like clusters, small (×10 lens), spinulose, black-pigmented, often becoming confluent or eroding. Isidia and soredia absent. Apothecia and pycnidia not known. TLC: (1) norstictic acid, salazinic acid, usnic acid; (2) no medullary substances, usnic acid.

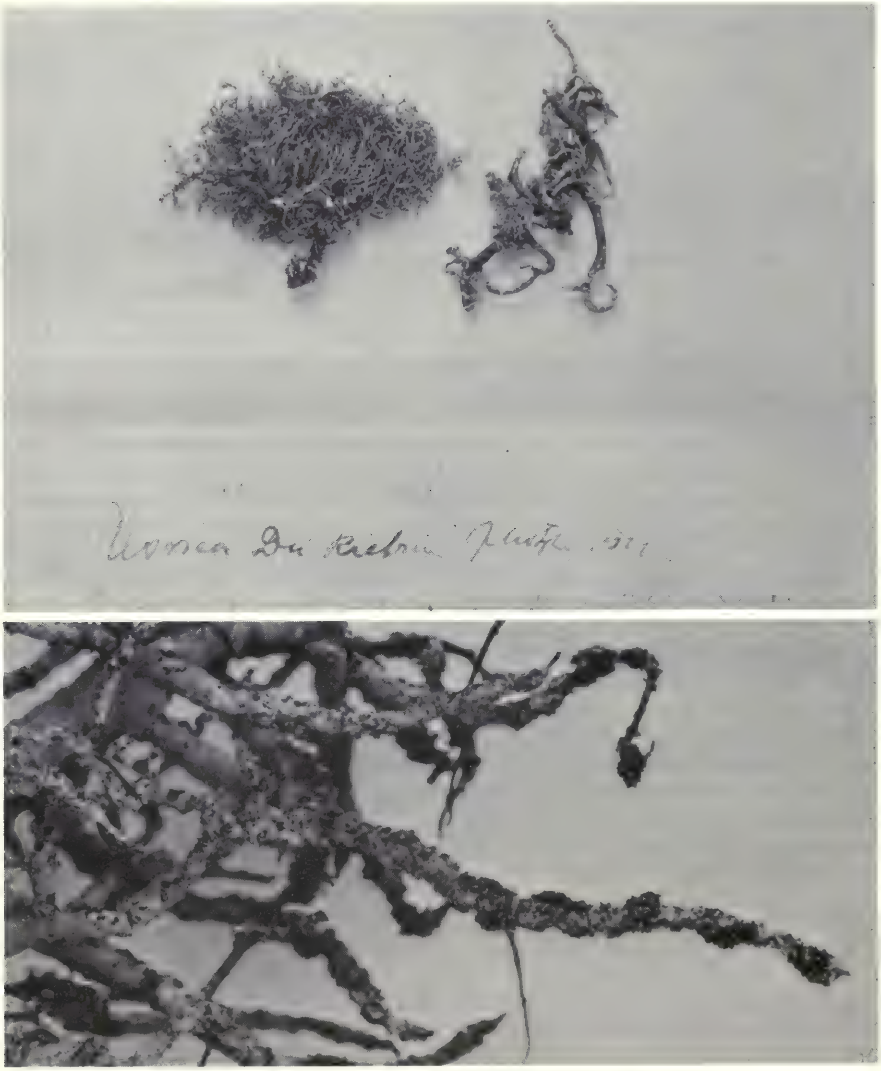


Fig. 22 *Usnea durietzii.* Top. Holotype of *Usnea durietzii* Motyka (UPS) ×1. Bottom. Detail of pseudoisidia. Peru, Ancash, July 1979, *Gibby & Barrett* (BM) ×10.

Distinguishing features: *Usnea durietzii* is characterised by its erect, often stalked, tufted habit, with short, irregular laterals and inflated, articulated main branches; a smooth, matt surface with numerous clustered, pigmented pseudoisidia which give a sooty appearance to the thallus; and a lax medulla, usually containing both norstictic and salazinic acids.

Distribution: *Usnea durietzii* has a rather disjunct, predominately western distribution throughout the Andean Cordillera from Panama and northern Venezuela to the Magellan Straits and Tierra del Fuego, although the species is very rare in Chile and Argentina, virtually being replaced there by *U. patagonica*. The species is characteristic of dry, exposed, rather than necessarily alpine, habitats. It is usually confined to high altitudes, *c.* 3000–4000 m, rarely occurring at lower levels towards the southern limit of its distribution as, for example, in the type locality. It has previously been recorded from the east side of the Andes in Prov. Mendoza, Argentina (Räsänen, 1939), and an illustration of *Usnea* cf. *condensata* by Asahina (1967) from Patagonia is clearly this species. In southern Patagonia *U. durietzii* has been collected with *U. patagonica* and *U. trachycarpa* (*Santesson*, 525 S!, *Santesson* 1920, S!). Fig. 8.

Chemistry: *Usnea durietzii* is characteristically found to contain norstictic and/or salazinic acids (Race 1); depsidone-deficient populations (Race 2) are rare and are apparently confined to northern part of the range.

Variation: *Usnea durietzii* is a rather variable species with a wide range of growth forms resulting from the irregular, repeated branching which occurs at a short distance above the holdfast. Frequently there is a proliferation of ultimate branches producing an untidy, tufted, 'witches-broom'-like structure consisting of numerous recurved branchlets with pigmented apices. Sometimes the basal black, stalk-like structure is absent and the thallus proliferates directly with a cluster of laterals. Fibrils, such as occur in *U. amblyoclada* (Appendix I, p. 115) and *U. trachycarpa*, are absent. Pigmentation is confined to the thallus base and apices and to the pseudoisidia.

The degree of development of pseudoisidia is variable and they may be incompletely developed or erode to form soredia. The pseudoisidia are always black-pigmented and tend to be produced in soralia-like clusters dispersed throughout the thallus. Such pseudoisidia are larger than those of *Usnea patagonica* and consequently can be distinguished from the flatter, partially corticate structures that are sometimes produced in other asexual species.

Papillae are usually absent although they rarely occur on main branches in those specimens that are of uncertain taxonomic position, which seem to have affinities with *Usnea amblyoclada* or *U. sphacelata*. In these specimens the medulla is not so characteristically lax as in *U. durietzii*.

The holotype specimen (Fig. 22) is a grotesque, knarled form of the species with proliferating branchlets and eroded pseudoisidia, although it is still characterised by a lax medulla, matt surface and tufted habit. Isotype collections are more typical. As the species often grows in exposed situations some features in consequence may not be fully developed as, for example, laxness of the medulla or development of pseudoisidia.

Species concept: *Usnea durietzii* is here included in the subgenus by virtue of habitat, distribution, and pigmentation. Fertile material of the taxon, or the recognition of a fertile counterpart, is required in order to confirm this assumption. This is a well-defined species, which may have affinities with the subgenus *Usnea*, for example with *U. amblyoclada* and *U. nigropapillosa*. The distribution overlaps that of *U. amblyoclada* from which it may be distinguished by the lack of fibrils and pseudocyphellae and also by the presence of clustered pseudoisidia rather than scattered true isidia. It also occurs with *U. bogotensis* which is a much more robust, unpigmented species with conspicuous true soralia that are only rarely pigmented, a compact medulla, and prominent white annulations and reticulations.

Usnea durietzii has some affinities with *Usnea patagonica* but may usually be distinguished by habit, surface features, propagule size, and medullary chemistry (Table 3). The presence of pigmented pseudoisidia, rather than pale true isidia, distinguish the species from *U. acanthella*. It may be separated from other asexual species within the subgenus by differences in soralia and surface characters, and often by habitat and distribution.

Specimens examined

Race 1

PANAMA. Chiriqui: Chiriqui, volcano crater's edge, 3300–3450 m, 12 December 1948, *P. F. Scholander* 169534 (US, CANL 17249).

VENEZUELA. Merida: Valle del Mufafi, páramo de Mucuchies, Sierra Nevada, 3650–3750 m, 9 April 1975, *M. E. Hale & M. López Figueiras* 44650 (US); trail between Laguna Negra and Mucubají, Sierra Nevada, 3500 m, 8 April 1975, *M. E. Hale & M. López Figueiras* 44455 (US); Rangel, Sierra Nevada de Santo Domingo, páramo de Mucubají, close to Laguna Grande (Laguna de Mucubají), *c.* 3500 m, 11 October 1981, *M. Lindström* 526 (GB); [unlocalised], 5500 m, 1846, *Voyage de Funck & Schlim* 987 (PC).

COLUMBIA. Santander: Páramo del Almorzadero, 3970 m, 17–19 November 1978, *J. Aguirre* 1090 (U 387342b). Boyacá: Páramo de La Rusia, Laguna Negra, 3745 m, 14 December 1972, *A. M. Cleef* 7229 (BM); Sierra Nevada del Cocuy, Alto Valle Lagunillas, SE. of La Laguna Cuadrada, 4080 m, 26 November 1972, *A. M. Cleef & P. A. Florschütz* 5558 (U 390939), 5559 (U 390940).

ECUADOR. Pinchincha: Volcán Sincholahua, plateau along Rio Pita, *c.* 3600 m, 30 May 1973, *L. Holm-Nielsen* et al. 6655 (GB); Cerro Iliniza, *c.* 4400 m, 7 March 1972, *L. Arvidsson & D. Nilson* 945 (BM, GB). Cotopaxi: Cotopaxi National Park, *c.* 60 km SE. of Quito, Pampa de Limpios, 3900 m, 13 June 1976, *S. R. Gradstein, H. Sipman & T. de Vries* 164 p.p. (BM, U).

PERU. Ancash: Quebrada Honda, Cordillera Blanca, 4260 m, July 1979, *M. Gibby & J. Barrett* s.n. (BM). Junín: Huytapallana, above Huancayo, *c.* 4600 m, 19 May 1973, *B. Mullins* 25 (BM); Cerro de Pasco, Conceptión, 4260–4560 m, 1969, *B. Mullins* s.n. (BM). Cuzco: Huaya, Huaya Pass, above Cuzco, 4500 m, 14 June 1973, *B. Mullins* 29 (BM); Pisac, near Cuzco, 3700 m, 14 April 1973, *B. Mullins* 24 (BM); above Cuzco, 3500–3600 m, 16 June 1973, *B. Mullins* 30 (BM). Ayacucho: near Ninabamba, 3900 m, 25 May 1973, *B. Mullins* 27 (BM). Apurímac: between Picćas and Huancaramay, 1932, *M. M. Wood* s. n. (BM). Puno: prope Azangaro, June 1854, *W. Lechler Pl. Peruvianae* 1758 (BM, M).

BOLIVIA. La Paz: Copacabana, near Lake Titicaca, 3800 m, 10 July 1973, *B. Mullins* 31 (BM).

CHILE. Malleco: *c.* 32 km SW. of Angol, 16 February 1958, *W. J. Eyerdam* 10794 (BM, FH). Magallanes: Is. Grafton, I. Elisabeth [54°07′S: 73°11′W] (type locality); prope Sandy Point, *W. Lechler Pl. Magellanicae* 108 (M); Rio de los Cruzeros, 60 km NNE. of Punta Arenas, 26 April 1940, *R. Santesson* 1920 p.p. (S).

ARGENTINA. Mendoza: Las Heras, Quebrada del Portero Puerta, near Cacheuta, 1800 m, June 1939, *R. Leal* s.n. (LD). Tierra del Fuego: Ushuaia, small island in Beagle Channel off the town, 30 January 1940, *R. Santesson* 532 p.p. (S).

Unlocalised: 'Jahina', Peruviae, *W. Lechler Pl. Magellanicae* 139 (M).

Race 2

VENEZUELA. Merida: [unlocalised], 1842, *Funck & Schlim* 9 & 7 (BM, PC); *Hale & López Figueiras* 44650 p.p. (as Race 1) (US); Rangel, Sierra Nevada de Santo Domingo, páramo de Mucubají, close to Laguna Grande (Laguna de Mucubají), *c.* 3500 m, 11 October 1981, *M. Lindström* 519 (GB); Páramo de Mucubají, on highest point of road Merida-Caracas, track from Laguna de Mucubají to Laguna Negra, 3500 m, 24 January 1979, *H. Sipman & M. López Figueiras* 11289 (U).

COLUMBIA. Cundinamarca: prope Bogotá, *J. Weir* 12 (BM).

BOLIVIA. Larecaja: near Sorata, Rampe de l'Apacheta, 4500 m, 1857, *G. Mandon Pl. Andinum Boliviensium* 1737 (BM, PC).

7. **Usnea neuropogonoides** Motyka **Fig. 23**

Lich. Gen. Usn. Stud. Monogr. **1**: 73 (1936). Type: Argentina: terr. Santa Cruz, Rio Fosiles, *c.* 1000 m, in rupibus, May 1905, *P. Dusén.* (UPS! – holotype). [TLC: no medullary substances, usnic acid.]

Description: Thallus up to 13 cm long, suberect to scrambling-prostrate, often lacking a distinct holdfast, divergent, ± dichotomous, infrequently branched to form a lax, spreading habit, rarely with fibrils, with short, divaricate, capillaceous secondary branches with attenuate, subcornute apices. Branches ± terete, occasionally subinflated or slightly angular, yellow-green, minutely variegated or black-pigmented only at the apices. Cortex *c.* 100 μm. Surface matt, smooth to faveolate or papillate, often fracturing. Medulla broad, lax, or sublax, axis thin, occupying *c.* 0·25 of the branch diameter. Apothecia, pycnidia, soredia, pseudoisidia and isidia not known. TLC: (1) psoromic acid, ± 2′-O-demethylpsoromic acid, ± fatty acids (murolic acid complex), usnic acid; (2) depsidone deficient, ± fatty acids (murolic acid complex), usnic acid.

Distinguishing features: *Usnea neuropogonoides* is characterised by its lax, suberect to scrambling habit, divergent branching, scant pigmentation, faveolate to papillate surface, lax medulla often containing psoromic acid, and lack of sexual or vegetative propagules.

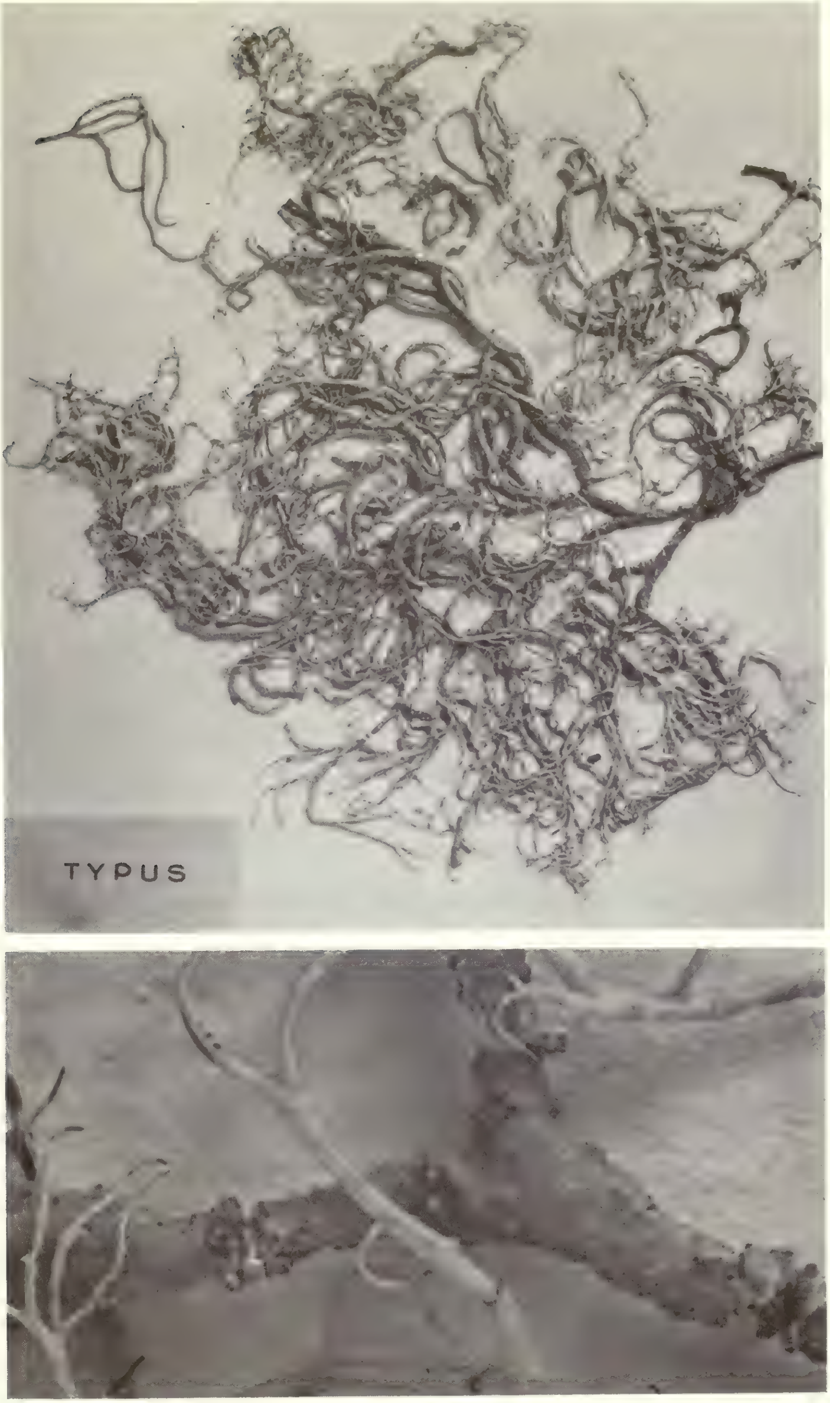


Fig. 23 Holotype of *Usnea neuropogonoides* Motyka (UPS). Top. Whole thallus ×1. Bottom. Detail of branching ×10.

Distribution: *Usnea neuropogonoides* is only known from a few collections from Patagonia, and is apparently characteristic of the windswept mesetas to the east of the Andean Cordillera. Fig. 8.

Chemistry: From the few collections (six) examined it appears that thalli more frequently contain psoromic acid (Race 1) than lack depsidones.

Traces of two or three fatty acids of the murolic acid complex were found in some thalli.

Variation: It is difficult to assess the extent of variation in this species from the few extant collections. The suberect or sprawling habit and loosely interwoven branches with pigmented apices appear to be constant. Pigmentation is scarce on the main branches, being confined to fractures and, rarely, papillae, thus bearing resemblance to the rare, straggling forms of *Usnea aurantiaco-atra*. Although fibrils are infrequent, the surface faveolation and papillation, the sublax medulla, and the thin axis are reminiscent of some of the variation found in *U. trachycarpa*.

The lack of reproductive structures suggests that this species is possibly disseminated by thallus fragmentation or by abrasion of fibrils or papillae. One specimen from Fuegia, 'San Isideo Point' (BM!), cited by Crombie (1876*b*), possibly belongs to this species, but is somewhat moribund and has a partially eroded cortex which could indicate the incipient production of isidia or pseudoisidia. Occasionally, in other thalli, nodular, white, soralia-like outgrowths are formed on main branches as a result of cortical damage or thallus fracture; these are anomalous structures and do not appear to have any taxonomic significance.

Species concept: *Usnea neuropogonoides* is included in *Neuropogon* since, although sterile, it has several characteristic features of the subgenus. Examination of further material may prove that this is an extreme form of another species, the most likely being *U. trachycarpa*, or that it even belongs to the subgenus *Usnea*, only producing pigmentation in very exposed habitats or when moribund as is seen in *U. torulosa* (p. 120).

The presence of papillae and depsidones rather than depsides (i.e. divaricatic acid) and different habitat requirements, indicate that although superficially similar, this species should not be included in *Protousnea* as delimited by Krog (1976). In addition, the main branches remain virtually terete and do not become so markedly angular in section or inflated at branch points, as, for example, in *P. scrobiculata*. However, in spite of this, certain similarities do exist, notwithstanding the limited morphological characters, which also define *Protousnea*.

Usnea neuropogonoides can be distinguished from decumbent forms of other *Neuropogon* species by the matt, faveolate to papillate surface, thin axis, broad, sponge-like, more or less lax medulla, and lack of propagules.

Specimens examined
Race 1
ARGENTINA. Santa Cruz: Lago San Martin, 4 February 1903, *P. Dusén* s.n. (H); between Lago San Martin and Lago Viedma, 2 February 1903, *Spegazzini* s.n. (BM, H); Chilean border, Lago San Martin, Laguna Theuen Aiken, [48°–49°S], 4 February 1903, *C. Hoberg* 121 (BM); Estancia Librun, [*c.* 51°S: 71°E], Shipton Exped. 1958–59, *P. W. James* s.n. p.p. (BM).
Race 2
ARGENTINA. Santa Cruz: Belgrano Pass, 22 December 1908, *C. Skottsberg* (UPS); Estancia Librun (as Race 1), *P. W. James* s.n. p.p. (BM).

8. Usnea patagonica F. J. Walker, **sp. nov.** **Fig. 24**

Diagnosis: Thallus fruticosus, pigmento nigro in cortice ad apices basimque suffusus. Rami extensi teretes saepe fibrillosi, papillis sparsis vel numerosis. Medulla sublaxa. Soralia pseudoisidiis minutis nigrescentibus excavata. Apothecia ignota. Acidum usnicum continens, et ± acidia aliphatica ad acidum murolicum pertinentia. Typus: Argentina, Santa Cruz, Patagonia, Lago Argentino [49°80′–51°S: 72°–73°30′W], Cordillera Cristales, 2000 m, on boulder in valley, 26 December 1958, *P. W. James* 31 (Shipton Exped.) (BM! – holotype; UPS!, US! – isotypes). [TLC: 3 fatty acids of the murolic acid group, usnic acid.]

Description: Thallus 1·5–3(–4–6) cm, arising from a delimited, pigmented holdfast, erect, ± subdichotomous, richly branched a short distance above, with numerous, clustered, inter-

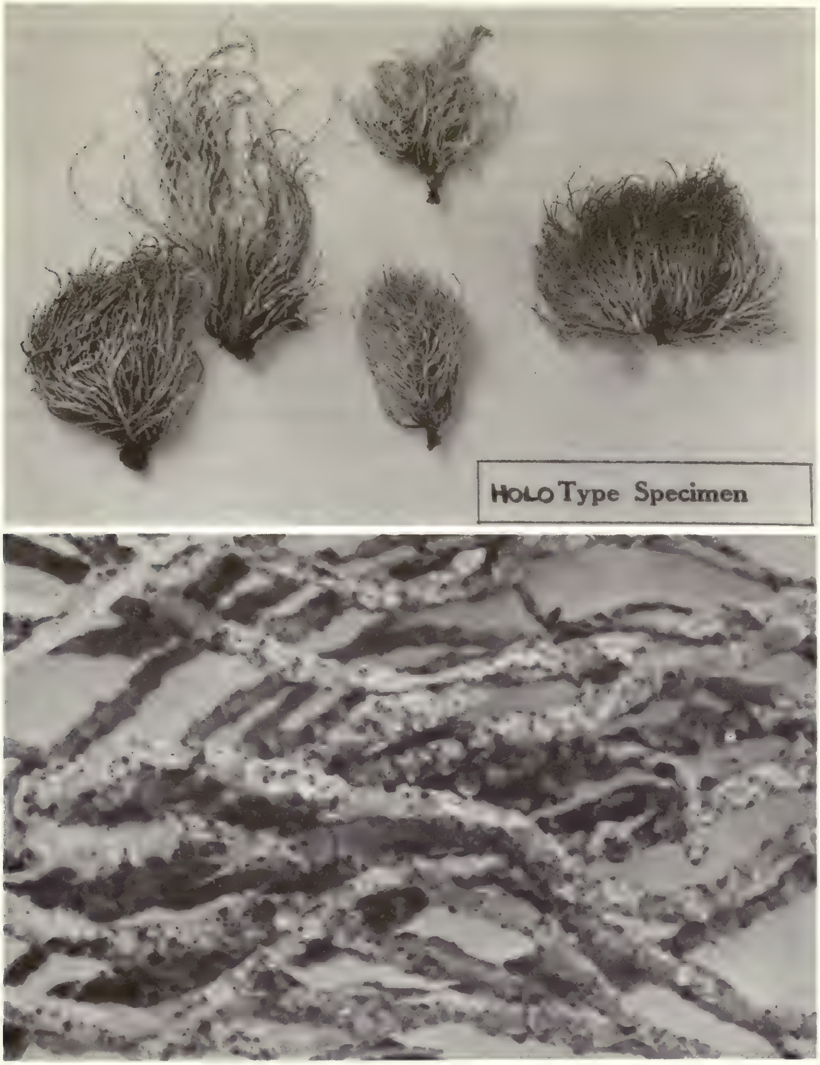


Fig. 24 Holotype of *Usnea patagonica* F. J. Walker (BM). Top. Whole collection ×1. Bottom. Detail of eroded soralia with pseudoisidia ×10.

woven, extended lateral branches, ± fibrils and capillaceous, ± flaccid ultimate branches. Branches terete, greenish yellow, black-pigmented only at or towards the apices. Cortex thin, 50–75 μm. Surface subnitid, subfaveolate-papillate (×10 lens) then scabrid, occasionally rupturing. Medulla lax or sublax, at least towards axis, axis thick, occupying *c.* 0·5–0·6 of the branch diameter. Soralia extensive ± throughout thallus, plane, ± irregular or ulcerose, rarely becoming effuse to confluent and excavate, arising from small papillae, ± an inconspicuous margin, with numerous, minute (×10 lens), pigmented pseudoisidia. Soredia rare, true isidia absent. Apothecia and pycnidia not known. TLC: no medullary substances, ± 1–4 fatty acids (murolic acid complex), usnic acid.

Distinguishing features: Usnea patagonica is characterised by its erect, richly branched, touselled habit with extended, lateral branches which rarely bear fibrils; a subnitid, subpapillate surface with numerous, minute, pigmented pseudoisidia, produced in ulcerose soralia, which give the thallus a dusted, sooty appearance, and a sublax medulla, frequently containing fatty acids.

Distribution: *Usnea patagonica* is mainly confined to the southern half of South America and is a species of the transitional arid-montane zone, frequently between the altitudes 500–1500 m, often occurring with *U. trachycarpa* and, less frequently, with *U. durietzii* or even *U. perpusilla*, having a slightly more eastern distribution. *U. patagonica* has been most frequently collected from the region of the Patagonian Lakes, for example Lago Argentino, but is rare further north, and is known from a single collection from Bolivia. Specimens cited by Follmann (1965*a*) from central Chile also appear to belong to this species. A single collection from South Africa is tentatively assigned to this species. Fig. 8.

Chemistry: All specimens examined were depsidone-deficient, containing usnic acid and usually one to four fatty acids, of Rf classes TDA 2–4, HEF 3–4, belonging to the murolic acid complex, which also occurs in *Usnea trachycarpa*. The presence of these fatty acids and lack of a depsidone-containing race may be regarded as additional characters for recognising *U. patagonica* as a distinct species. Traces of the UV+ unknowns are occasionally present.

Variation: The general form of *Usnea patagonica* shows little variation apart from the extent of production of secondary branches and extended laterals, which usually replace fibrils. In a single gathering thalli may either bear numerous, capillaceous, ultimate branches or may entirely lack laterals and instead have truncated apices. Thalli are characteristically repeatedly branched, sometimes a short distance above the blackened holdfast, giving a tufted, tasselled habit.

The surface may be subnitid to waxy, and in smaller, immature thalli, is occasionally devoid of papillae which lack pigmentation. Rarely annulations are formed resembling those of *Usnea acromelana*, although in *U. patagonica* this is usually confined to the finer, laterals rather than main branches.

The laxness of the medulla may vary, but even when not well developed, the hyphae are more loosely interwoven in the proximity of the axis. Such variation is similar to that found in *Usnea trachycarpa*; the primary branches do not become inflated as in *U. durietzii*.

There is little variation in the form of the soralia; the production of small, pigmented pseudoisidia is a characteristic feature of the species. The pseudoisidia are rarely as well-developed as in *Usnea durietzii* and arise in more or less delimited, discrete soralia which rarely become confluent as in that species. Occasionally, soralia may resemble the less well-developed forms found in *U. antarctica*, but generally they are more eroded in *U. patagonica* and lack the distinctive crateriform margin. Table 3 summarises the differences between these three species and Fig. 3 illustrates their asexual propagules.

Black pigmentation is normally confined to the holdfast, pseudoisidia, and branch apices, although the ultimate branches may rarely be variegated or extensively pigmented.

High altitude material from Cedarberg, South Africa (*Schelpe* 1961, BOL!, CANL 16944!), originally determined by Lamb as *Usnea acromelana*, very closely conforms to *U. patagonica*, and is tentatively included in this species. Some thalli have a blackened base, are richly branched above with pigmented apices, and have excavate, ulcerose, soralia-like areas which contain small, pigmented pseudoisidia. Thalli also lack diagnostic medullary substances, containing traces of three to five fatty acids of the murolic acid complex. Other thalli in the same collection do not resemble *U. patagonica* so closely, and may belong to another taxon, since they are less extensively pigmented, have more fibrils, a markedly faveolate surface, and a laxer medulla lacking fatty acids. However, they do possess similar soralia-like areas that, less frequently, produce poorly developed pseudoisidia.

Species concept: Many specimens of *Usnea patagonica* have been previously determined as *U. acromelana* or *U. durietzii* according to the extent of pigmentation, branching, or development of pseudoisidia. In many respects this species might be regarded as an intermediate entity between several asexual species that occur in South America, and is, for these reasons, included within the subgenus despite the lack of fertile material.

Usnea patagonica appears to be most closely related to *U. durietzii* with which it shares many common features. The two species may be distinguished by differences in their habit and branching which, in *U. durietzii*, is much more irregular with the production of clusters of fibril-like, stunted branchlets rather than fine, extended laterals of *U. patagonica*. In *U.*

patagonica branches are never inflated and pseudoisidia are less prominent. The holotype of *U. durietzii* is very close to, but distinct from, more robust forms of *U. patagonica* and, in addition, contains traces of norstictic acid.

The presence of fatty acids rather than depsidones, preferred habitat and distribution may, conversely, indicate affinities between *Usnea patagonica* and Race 3 of *U. trachycarpa* with fibrils of the latter species being replaced by extended laterals bearing soralia. In contrast, the general habit of the new species is similar to depauperate forms of *U. antarctica* from the South Orkney and South Shetland Islands, although the thallus is less robust with somewhat flaccid ultimate branches. The extent of pigmentation is also similar and is frequently sparse; unlike the majority of specimens of *U. antarctica* the thallus always has a blackened basal portion above the holdfast.

Usnea patagonica may be distinguished from *U. subantarctica* and *U. sphacelata* by the form of the soralium, presence of pseudoisidia, less extensive pigmentation, and different ecological parameters; from *U. acromelana* by the presence of papillae and pseudoisidia, a laxer medulla and by fewer, usually unpigmented, cortical annulations.

Specimens examined

BOLIVIA. La Paz: Prov. Murillo, Valle de Chuquiaguillo, Incachaca, 4200 m, 7 April 1921, *E. Asplund* 56 (UPS).

CHILE. Santiago: Cordillera Central, SW., 3000 m, 1964, *G. Follmann* 13446-L (LD), 13435-L (KASSEL), 13442-L (UPS), 13443-L (UPS). Cautín: Cordillera Lonquimay, 2050 m, 4 November 1930, *R. P. A. Hollermayer* s.n. (H). Aisén: Estancia Ñirehuao, Bãno Nuevo, 23 September 1940, *R. Santesson* 5010 p.p. (S), 5021 (S); Estancia Ñirehuao (25–30 km N. of Rio Coyhaique), 20 November 1940, *R. Santesson* 4821 (S), 25 November 1940, *R. Santesson* 4865 (S); Estancia Coyhaique Alto (near Cerro Coyhaique), *c.* 100 m, 18 November 1940, *R. Santesson* 4632 p.p. (S); Coyhaique Alto, 1000 m, 18 November 1940, *R. Santesson* Lich. austroam., ex herb. Regnelliano 423 p.p. (C, H, M, S); Coyhaique, Cerros Divisaderos (Cordon de Bella Vista), 1200 m, 13 November 1940, *R. Santesson* 4435a (S), 4435b (S, UPS). Magallanes: Rio de los Cruzeros (60 km NNE. of Punta Arenas), 26 April 1940, *R. Santesson* 1920 p.p. (S); Natales, Cerro Dorotea, 9 May 1940, *R. Santesson* 2137 p.p. (S), 8254 p.p. (S); Lago del Toro (Lago Maravilla), La Peninsula, 10 March 1941, *R. Santesson* 6325 (S); Tierra del Fuego, Isla Navarino, 300 m, 1963, *G. Follmann* 14591 (UPS), 13978 (KASSEL), 14587 (KASSEL), 14586 p.p. (M); 14589 (LD); Isla Navarino, Puerto Navarino, 10 m, 28 February 1940, *R. Santesson* 1234a (S, UPS); Paine National Park, Lake Pehoe, 129 km N. of Puerto Natàles, 18 m, 11 March 1974, *C. Neher* 76 (LAM 202156).

ARGENTINA. Río Negro: Cerro Leones, near summit, W. bank of Lago Nahuel Huapí, 1 January 1974, *A. Henssen & G. Vobis* 24625 (MB); Parque Nacional Nahuel Huapí, Cerro Catedral, Liftstation, *c.* 2225 m, 6 January 1974, *A. Henssen & G. Vobis* 24674f p.p. (MB); Cerro Otto, *c.* 10 km W. of San Carlos de Bariloche, 1200 m, 29–30 December 1980, *K. Kalb* s.n. (herb. Kalb). Santa Cruz: Lago Viedma, 2 February 1903, *P. Dusén* s.n. p.p. (H); N. coast of Lago Viedma, 1200 m, 2 April 1903, *Hoberg* 123 (BM); Lago Argentino, Calafate, weg nach Punta Bandera, Campo Anita Fuss des Cerro Moyano, 300–400 m, 20 December 1973, *A. Henssen & G. Vobis* 24535d (MB); Calafate, Cuevas de Hualichu, 18 December 1973, *A. Henssen & G. Vobis* 24523a (MB); near Calafate, 1959, *P. W. James* 4/120b (BM); Parque Nacional Los Glaciares, Lago Roca, Jeronima, 16 December 1973, *A. Henssen & G. Vobis* 244991 (MB); Lago Roca, Cordon de los Cristales, *c.* 1000 m, 26 December 1958, *P. W. James* s.n. (BM); Cordillera Cristales (type locality); Lago Roca *c.* 1000 m, December 1958, *P. W. James* 16 (BM); 20 (BM); Lago Roca, Cerro del Fraile, January 1959, *P. W. James* s.n. (BM); Rio Fosiles, *c.* 1000 m, April 1905, *P. Dusén* s.n. p.p. (M, WU 2997); Uppsala Glacier, Estancia La Christina, 16 December 1958, *P. W. James* 5/49 p.p. (BM), 5/10 (BM). Tierra del Fuego: Ushuaia, La Peninsula, 3 January 1940, *R. Santesson* 559 p.p. (S); Sierra Sorondo, N. slope above Las Cotorras (*c.* 20 km ENE. of Ushuaia), 800 m, 6 February 1940, *R. Santesson* 641f p.p. (S); Sierra Alvear, S. slope, above Las Cotorras, 700 m, 9 February 1940, *R. Santesson* 637b (UPS).

Uncertain determination

SOUTH AFRICA. Cape Province: Cedarberg. Between Tafelberg (Table Mt.) and Spout, 1830 m, 18 January 1947, *E. Schelpe* 1961 p.p. (BOL, CANL 16944).

9. Usnea perpusilla (Lamb) F. J. Walker, comb nov. Figs 25–26

Neuropogon perpusillus Lamb in *J. Linn. Soc.* (Bot.) **52**: 234 (1939). Type: Chile, Pico de Pilque, prope Antuco, *Poeppig* Pl. Chil. III, 278(56) (BM! – holotype; B, G – ?isotypes (Motyka, 1936), not seen). [TLC: no medullary substances, usnic acid.]

Neuropogon rohmederi Lamb in *Lilloa* **14**: 158 (1948). – *Usnea rohmederi* (Lamb) Lamb in *An. Parq. nac. B. Aires* **7**: 157 (1959) ['1958']. Type: Argentina, Chubut, Lago Futalaufquen, 1800–2000 m, 1945, *G. Rohmeder* (LIL 2275 – holotype, not seen; BM!, CANL 17205!, H!, UPS!, US! – isotypes). [TLC: no medullary substances, ± UV+ unknowns, usnic acid.]

Neuropogon rohmederi f. *ushuaiensis* Lamb in *Lilloa* **14**: 160 (1948). Type: Argentina, Tierra del Fuego, Sierra Alvear, the southern slope, above Las Cotorras (*c.* 20 km ENE. of Oshuaia), 900–1000 m, 7 February 1940, *R. Santesson* 640c (640a p.p.) (S! – holotype; CANL 17209!, UPS! – isotypes). [TLC: no medullary substances, usnic acid.]

Description: Thallus (2)–5–10(–14) cm, arising from a proliferating or rarely delimited, unpigmented, holdfast, erect, ± dichotomous, infrequently to richly branched above. Branching often divergent with short, subcapillaceous, sometimes shortly attenuate then deflexed, laterals. Fibrils very rare. Branches terete, yellow-green, ± variegated with bands of violaceous black pigment, ± continuously pigmented towards the apices. Cortex variable in thickness. Surface smooth, subnitid to waxy, ± incomplete fractures, often becoming markedly faveolate, never verrucose, rarely ± scabrid with minute, pigmented papillae (×10 lens). Medulla lax, rarely sublax, axis thin occupying 0·25–0·5 of the branch diameter. Soredia, pseudoisidia and isidia absent. Apothecia frequent, 1–8(–12) mm diameter, lateral, subsessile, often in series, rarely subterminal with a geniculate spur, ± reniform or irregular on maturity. Disc black, excipulum smooth to faveolate-reticulate, margin thin, often ± excluded, rays rare. Pycnidia rare. TLC: (1) psoromic acid, ± 2′-O-demethylpsoromic acid, ± 1 to 4 UV + unknowns, usnic acid; (2) no medullary substances, ± 1 to 4 UV+ unknowns, usnic acid.

Distinguishing features: *Usnea perpusilla* is characterised by its erect, moderately branched thallus, often extensively pigmented towards the apices, a more or less smooth, waxy, subfaveolate surface, a lax medulla normally lacking medullary substances, a thin axis, and lateral or rarely subterminal apothecia with a black disc, with a faveolate-reticulate excipulum, usually lacking marginal rays.

Distribution: *Usnea perpusilla* is confined to the Andean Cordillera in southern South America, occurring in Argentina and Chile from Tierra del Fuego northwards to about latitude 37°S. It is characteristic alpine-southern temperate species, often found at high altitudes, between 1000 and 2000 m, in communities with such species as *U. aurantiaco-atra* and, occasionally, *U. trachycarpa* and *U. patagonica*. Fig. 7.

Chemistry: The majority of specimens examined lack medullary substances although some may contain localised high concentrations of three or even four UV+ unknowns (p. 15). Specimens containing psoromic acid (Race 2) are only known from a single locality towards the northern limit of the distribution of the species.

Variation: *Usnea perpusilla* is a moderately variable species exhibiting a range of growth form, branch anatomy, and apothecial form. The size of the thallus is very variable, ranging from small thalli, *c.* 2 cm, which bear small, cupular apothecia, as in the type specimen, to larger, *c.* 14 cm, erect forms that may become subdecumbent. The extent of branching is also variable, ranging from almost monopodial forms arising from a proliferating holdfast to lax, spreading forms, arising from a delimited holdfast, as in the type of *U. rohmederi*. Where branching is extensive the thallus may produce short, fibril-like, recurved, subcapillaceous, ultimate branches.

Specimens recently collected from Prov. Río Negro, Argentina (herb. Kalb!, BM!) illustrate well two features of the variation found in this species; namely, seemingly superficial morphological similarities to *Usnea ciliata*, and an intermediate range of thallus size between the types of *U. perpusilla* and *U. rohmederi*.

The main branches are usually unpigmented near the base, with apices and secondary branches being either conspicuously variegated or continuously pigmented violaceous black towards the tips.

The surface is characteristically smooth and waxy and may become faveolate or slightly inflated if the underlying medulla is very lax. In such instances the cortex may fracture forming incomplete, unpigmented annulations that are not a constant diagnostic feature as in *Usnea*

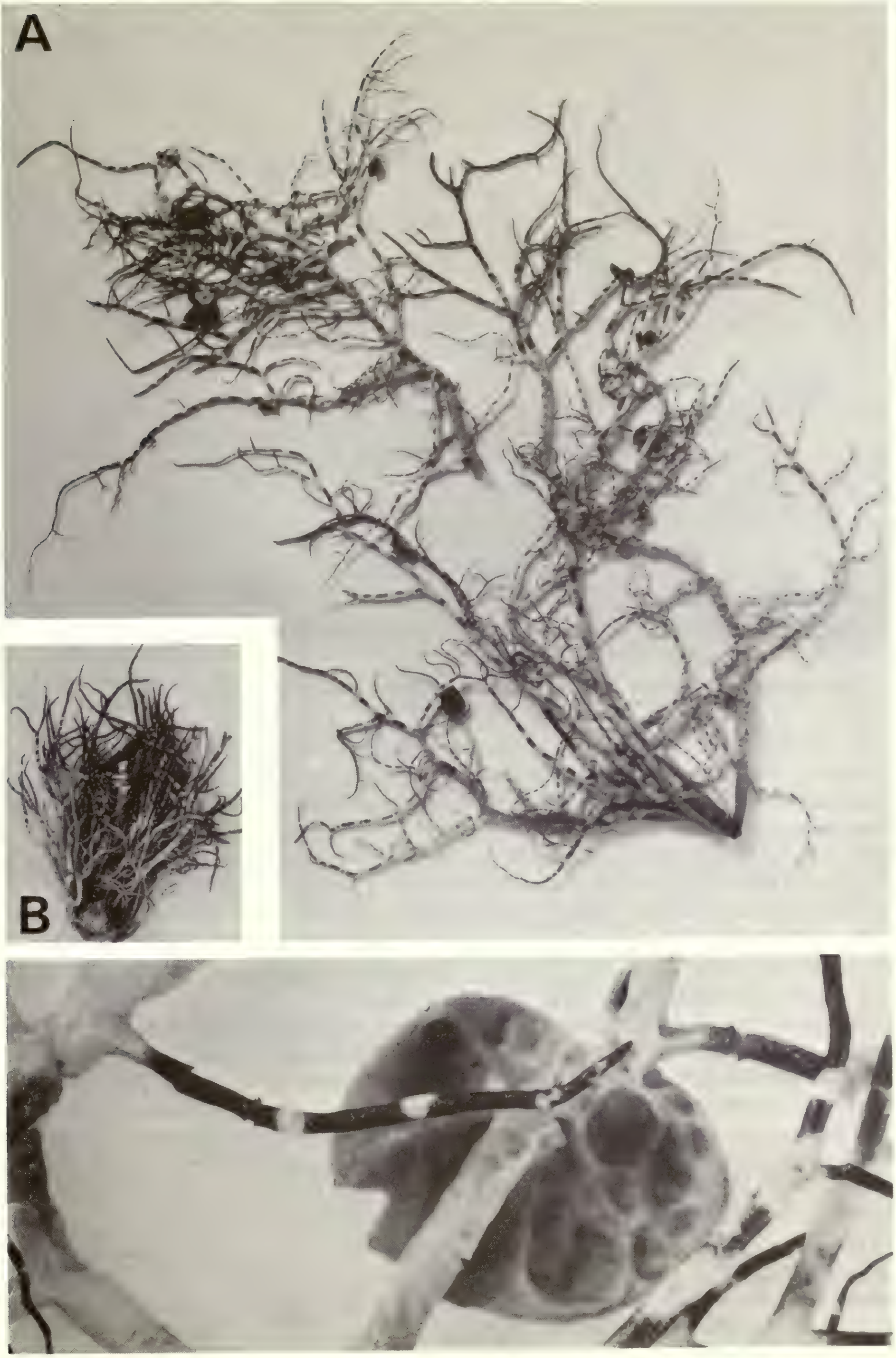


Fig. 25 *Usnea perpusilla.* A-Isotype of *Neuropogon rohmederi* Lamb (CANL). Top. Whole thallus ×1. Bottom. Detail of excipulum ×10. B(inset)- Holotype of *Neuropogon perpusillus* Lamb (BM) ×2.

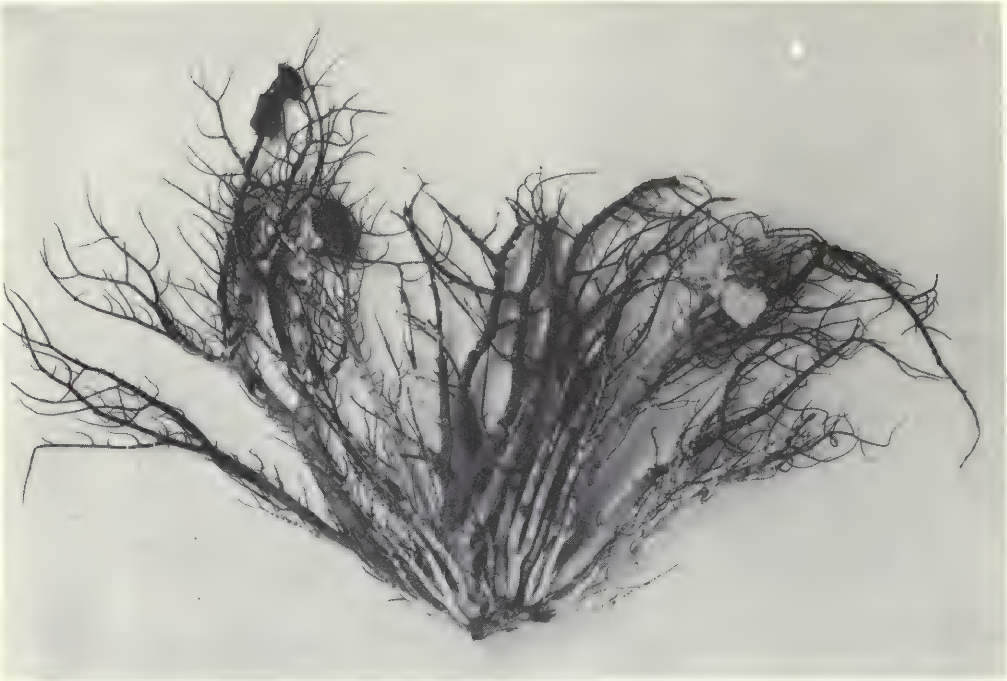


Fig. 26 *Usnea perpusilla.* Isotype of *Neuropogon rohmederi* f. *ushuaiensis* Lamb (CANL) ×1·5.

ciliata. The thallus is never strongly verrucose-papillate, as in *U. aurantiaco-atra*, and only rarely, in more robust forms where fibrils are present, do small, usually black-pigmented, papillae occur, giving the thallus a slightly scabrid texture, as in the type of *U. rohmederi* f. *ushuaiensis* (Fig. 26).

Typically the axis is very thin in main branches, occupying about a third of the branch diameter. The degree of laxness of the medulla is very variable, and in some instances may only be looser and arachnoid in close proximity to the axis. Specimens in which the medulla is more compact and where the axis correspondingly occupies a greater proportion of the diameter, have previously been mistaken for *Usnea ciliata* or *U. aurantiaco-atra*; they may usually be distinguished from these species by other well-defined characters.

Positioning and size of apothecia may vary in *Usnea perpusilla*. In well-developed thalli the apothecia are often produced serially along a branch, a feature more rarely encountered in other fertile species, for example *U. ciliata* and *U. aurantiaco-atra*. Less frequently, in more richly branched thalli, the apothecia are subterminal, and then often have a geniculate subtending spur which may in turn produce additional apothecia, thus reflecting the characteristic habit of the species. The apothecia are subsessile, having a broad area of attachment; frequently various stages of development may be observed on a single branch, ranging from a small, rounded, cupular form to the more typical reniform shape with a deflexed, irregular outline and a virtually excluded thalline margin. Faveolation of the excipulum is usually a constant feature. Marginal excipular rays are infrequent and, when present, may vary in number, length and extent of pigmentation. Their formation may be correlated with the extent of branching since they are most likely to be present in richly branched specimens.

Species concept: Examination of the type specimens of *Usnea perpusilla* and *U. rohmederi*, including f. *ushuaiensis*, and study of additional material has shown that these taxa fall within the variation of a single species. The holotype of *U. perpusilla* (BM!) is very fragmentary (Fig. 25), although additional collections (M!, PC!) that may be part of Poeppig's original gathering, are better developed. Examination of slides of sections of the holotype prepared by Lamb (BM!) show that mature asci are very rare, an indication that apothecia are in fact immature, and that the medullary tissue, although not expanded, shows signs of becoming arachnoid-lax in the proximity of the axis.

Lamb (1948*a*) separated *Usnea rohmederi* f. *ushuaiensis* on the presence of minute, pigmented papillae, an almost smooth excipulum with marginal rays, and slight differences in spore size and thecium height, all of which are here accepted as infraspecific variation. *Usnea perpusilla* has often previously been mistaken for *U. ciliata* and may be distinguished by the lax medulla, absence of conspicuous, pigmented annulations, a frequently variegated, rather than continuously pigmented, thallus, and often by the serial position of the apothecia. (Fig. 2). The two species have a marked difference in distribution. In *U. ciliata* apothecia are normally terminal or sublateral, also with a geniculate spur, whilst in *U. perpusilla* they are more frequently produced laterally, often up to five in series, with a much broader area of attachment, sometimes producing an acute geniculation of the branch.

Forms with fibrils may be distinguished from *Usnea trachycarpa* by the difference in disc colour; the species can be distinguished from *U. aurantiaco-atra* by the degree of ornamentation and differences in branch anatomy.

Specimens examined
Race 1
ARGENTINA. Río Negro: Cerro Rigi, near Lago Frias, *c.* 1750 m, 15 February 1950, *I. M. Lamb* 6046 (CANL 17016, UPS).
Race 2
CHILE. Bío Bío: 'in summ. And. cacum.'. *Kunze* s.n. (M); In cacum. montis, Pico de Antuco, 1835, *Kunze* s.n. (PC); Pico de Antuco, ex Kunze, s.n. (PC); *Poeppig* Pl. Chil. III [*c.* 37°S] (type locality). Cautín: Cordillera Lonquimay, 2050 m, 4 November 1930, *R. P. Hollermayer* s.n. (H). Unlocalised: 'Chil. bor. rupes marit.' *Poeppig* s.n. (PC).
ARGENTINA. Neuquén: Cordillera Suangulo [38°–41°S], 2130 m, 16 January 1926, Kew Andes Exped., *H. F. Comber* 470 (BM, E); Paso Pino Hachado – Lonquimay [Chilean Border], 1900 m, 10 January 1948, *A. Pfister* 8123 (CANL 17014, UPS); Parque Nacional Nahuel Huapí, Brazo Rincón, Cerro Dormilon, *Pérez Moreau* 6793 p.p. (BM, H), 2 February 1940, *Pérez Moreau* 4543 p.p. (H); Parque Nacional Lanín, Cerro Malo, N. of Lago Lacar, *c.* 1900 m, 28 January 1968, *J. H. de Haas* 1290-A (U 313666b). Río Negro: Parque Nacional Nahuel Huapí, Cerro Rigi, Lago Frías, 23 January 1940, *Pérez Moreau*, s.n. (S); *I. M. Lamb* 6046 (as Race 1) (BM, UPS); Parque Nacional Nahuel Huapí, Cerro Catedral, Liftstation, *c.* 2225 m, 6 January 1974, *A. Henssen & G. Vobis* 24674f (MB), 24677d (MB), 24677g (MB); Parque Nacional Nahuel Huapí, Cerro Catedral, *c.* 20 km SW. of San Carlos de Bariloche, 1850 m, 2 January 1981, *K. Kalb* s.n. (herb. Kalb); Parque Nacional Nahuel Huapí, Cerro Catedral, near Bariloche, 2000 m, 10 February 1950, *I. M. Lamb* 5949 (BM, CANL 17206, FH, H, UPS), 5951 (CANL 17207, UPS), 5956 (CANL 17208), 5962 (CANL 36562), 5964 (CANL 36563); Parque Nacional Nahuel Huapí, Cerro Otto, *c.* 10 km W. of San Carlos de Bariloche, 1250 m, 29–30 December 1980, *K. Kalb* s.n. (BM, herb. Kalb); Parque Nacional Nahuel Huapí, Capitán, 30 April 1933, *E. & A. Ljungner* 1367 (S); Cerro Goye, 1670 m, 25 January 1944, *J. C. Montiel* s.n. (CANL 17204); Lago Nahuel Huapí, Puerto Manzano, 19 January 1966, *H. & F. Walter* 170 (M). Chubut: Chilean frontier [44°28′S: 71°34′W], 1500 m, 13 February 1902, *Hoberg* s.n. (BM); Lago Mendez, Cerro Torrecillas, *c.* 1000 m, 6 December 1940, *N. Kühnemann* 4792 (BM); Lago Futalaufquen, (type locality – *N. rohmederi*). Santa Cruz; Lago Viedma, *c.* 1400 m, Shipton Exped., January 1959, *G. C. Bratt* s.n. (BM, CHR 343330, FH); Lago Argentino, Cerro Mayo, Seno Mayo, *c.* 1100 m, Shipton Exped., February 1959, *P. W. James* s.n. (BM). Tierra del Fuego: Cerro [unlocalised] S. of Estancia 'La Marina', 500 m, 1921, *Argentina Faculty of Science Exped.* 564 p.p. (BM); Sierra Alvear (type locality – *N. rohmederi* f. *ushuaiensis*), 800–900 m, 7 February 1940, *R. Santesson* 639d (S); Sierra Sorondo, above Las Cotorras, *c.* 20 km ENE. of Ushuaia, 800 m, 6 February 1940, *R. Santesson* 641e (UPS, S); Monte Marcial, SE. slope, above Ushuaia, 700 m, 29 January 1940, *R. Santesson* 450c (UPS, S).

For further localities see Lamb (1948*a*).

10. **Usnea pseudocapillaris** F. J. Walker, **sp. nov.** **Fig. 27**

Diagnosis: Usneae subcapillari affinis, sed thallo minore et soraliis parvis punctiformibus differt; apothecia rara. Typus: New Zealand, South Island, Otago, Humboldt Mountains, Mt. Nox, 1950 m, 31

December 1969, *D. J. Galloway* (CHR 343226! – holotype; BM! – isotype). [TLC: norstictic acid, salazinic acid, ± protocetraric acid, usnic acid.]

Description: Thallus 2–3 cm, arising from a delimited, ± pigmented holdfast, erect, becoming subpendulous or subdecumbent. Brancing extensive, divergent, ± dichotomous, with numerous, delicate, capillaceous, spreading branches and short, attenuate, deflexed laterals; usually lacking fibrils. Branches terete, yellow-green, ± continously pigmented or variegated violaceous black towards the apices. Cortex thin. Surface smooth, waxy, epapillate, easily fracturing, forming ± regular, black-edged annulations. Medulla sublax towards the axis, axis occupying 0·3 – 0·5 of the branch diameter. Soralia small, punctiform, plane to concave or eroded. Soredia farinose, unpigmented. Pseudoisidia absent. Apothecia rare, immature, as in *U. subcapillaris*. Pycnidia not seen. TLC: norstictic acid, salazinic acid, ± protocetraric acid, usnic acid.

Distinguishing features: *Usnea pseudocapillaris* is characterised by its spreading to subdecumbent habit and a richly branched thallus with numerous, fragile, divergent, flexuose-capillaceous secondary branches bearing small, unpigmented soralia. This species also has a waxy, pigmented-annulate surface, and a sublax medulla containing depsidones.

Distribution: *Usnea pseudocapillaris* appears to be confined to the South Island of New Zealand, occurring in alpine habitats with other species of the *U. ciliata* complex. It is so far only known from a restricted area in Central Otago, lying within the distribution of *U. subcapillaris*, and a single locality in NW. Nelson. It is possible that this species may also occur in Tasmania, where both *U. acromelana* and *U. subcapillaris* are known. Some Tasmanian specimens examined are morphologically very similar to this species but, as they lack soredia and apothecia, they are therefore probably best regarded as immature thalli of *U. subcapillaris* (for example: Mt. Wellington, herb. Degelius A-414!) pending the discovery of more typical material. Fig. 6.

Chemistry: Only one chemical race, that containing norstictic and salazinic acids, has been detected. However, it is possible that other races may be discovered since both the related *Usnea subcapillaris* and *U. acromelana* have more than one chemical race.

Variation: The thalli of this new species are small, rarely exceeding 4–5 cm, are characteristically richly, dichotomously branched, and arise from a delimited holdfast. The fine, capillaceous, divergent secondary branches form a lax, subdecumbent, loosely-interwoven network, whose fragility is accentuated on storage in herbaria. The primary branches are frequently widely diverging and produce a characteristic angulose network of secondary branches which also occurs in *Usnea subcapillaris*; however, in *U. pseudocapillaris* these are not as extensive or extended.

The diameter of secondary branches may vary; typically they are short, capillaceous, 0·1–0·3 mm diameter, resembling those of *Usnea subcapillaris*. Rarely secondary branches may be up to 0·5 mm in diameter and in such instances there is a more gradual transition in width from main branches. In all specimens the ultimate branches are short, divergent or often reflexed and shortly attenuate, giving a netted appearance to the thallus. This is also a feature of richly branched forms of *U. acromelana* and less well-developed forms of *U. subcapillaris*. Formation of a secondary holdfast and ensuing regeneration may occur in this species, and in *U. subcapillaris*, where decumbent branches are in contact with the substrate, as for example in the holotype of this new species.

The smooth, waxy surface is characteristic of the *Usnea ciliata* complex, along with the rupturing of main branches to form black-edged annulations. Such annulations are more widely dispersed than in *U. acromelana*, although rarely absent; they tend to accentuate the characteristic divergent branching of the thallus. Occasionally the effect of the laxness of the underlying medulla in conjunction with cortical fracturing may give rise to partially inflated segments. The primary branches are usually unpigmented, apart from the annulations, whilst the extent of pigmentation in secondary branches ranges from complete blackening to narrow bands of variegation.

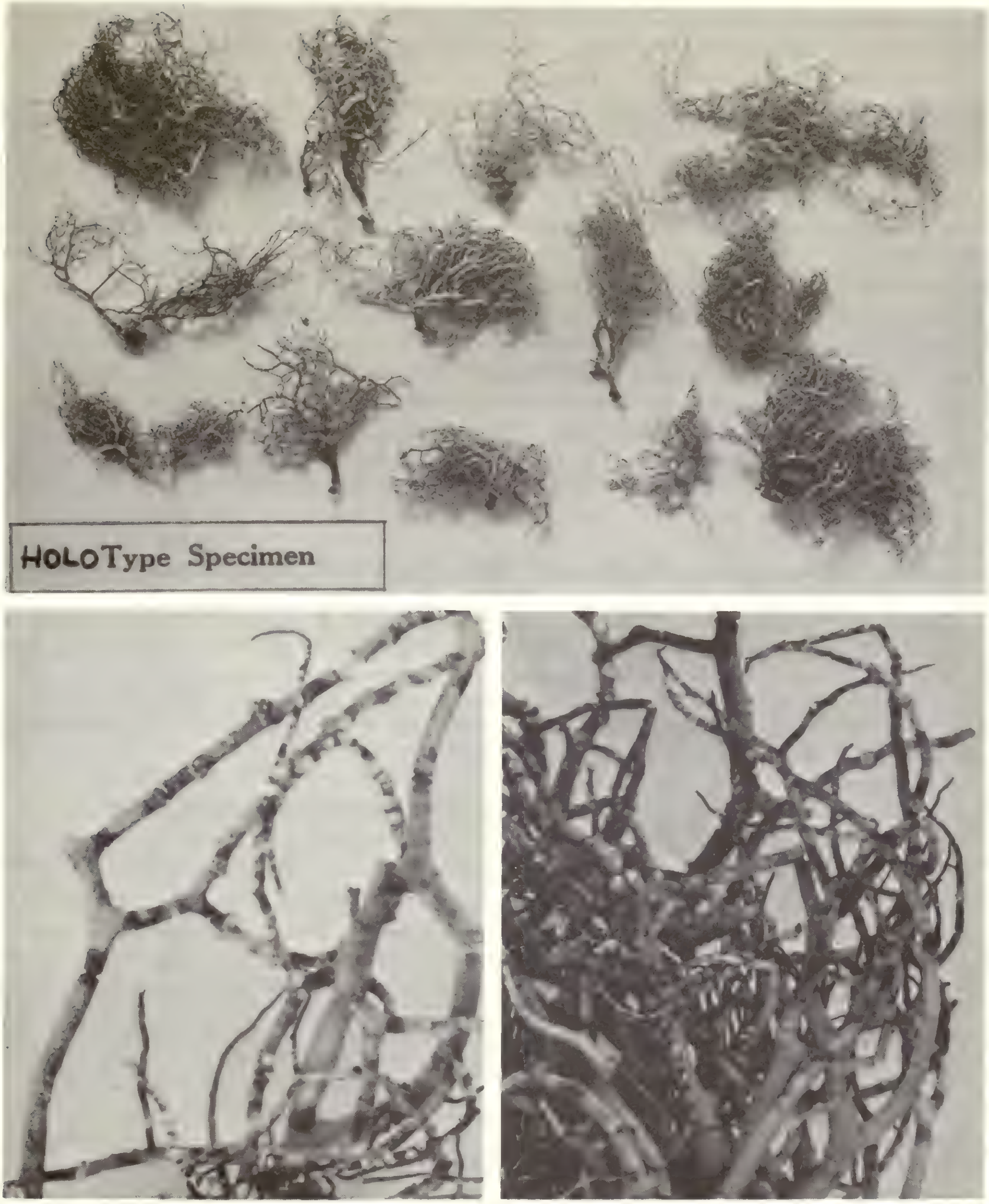


Fig. 27 Holotype of *Usnea pseudocapillaris* F. J. Walker (CHR). Top. Whole collection ×1. Bottom. Detail of branching and soralia ×10.

The soralia are usually minute and indistinct and only occasionally become convex, globose, confluent or pigmented in more robust specimens. The presence of soralia may account for the shorter and stouter nature of the secondary branches in this species when compared with *Usnea subcapillaris*.

Apothecia are extremely rare and only immature examples are known on two thalli which form part of the type collection.

Species concept: *Usnea pseudocapillaris* belongs to the *U. ciliata* complex and may be regarded as the sorediate counterpart to *U. subcapillaris*. Plants are generally smaller and slightly more erect than *U. subcapillaris* and have shorter, less trailing, secondary branches. Unlike *U. ciliata* and *U. subcapillaris* the delimitation between this species and *U. acromelana* may not always be so easily discerned, since occasional thalli exhibit intermediate characteristics. However, this is a rare occurrence and, despite the seemingly close relationship, the persistence of a distinct, divergent branching pattern, capillaceous secondary branches, and a much more flaccid, fragile nature are here considered to merit specific rank. It is generally possible to separate coarser specimens of *U. pseudocapillaris* from the finer forms of *U. acromelana* using a combination of some of the characteristic features of the former, even though a single thallus may not exhibit all these features. Short, divergent primary branches are typical of *U. pseudocapillaris*; more richly branched forms of *U. acromelana* tend to be more compact with less divergent branches which lack segmentation, and have more numerous, closely arranged annulations.

Usnea pseudocapillaris may easily be distinguished from typical forms of *U. acromelana* which are sparingly branched, erect, and arise from a proliferating holdfast, and from *U. antarctica* and *U. sphacelata* by differences in habit, branching, ornamentation, and medullary chemistry.

Specimens examined

NEW ZEALAND. South Island. Nelson: Kakapo Peak, *c.* 1520 m, 16 December 1982, *J. K. Bartlett* 25814 (herb. Bartlett, BM); Tasman Mountains, Douglas Range, *c.* 1400 m, 17 December 1983, *J. K. Bartlett* 36109d p.p. (herb. Bartlett, BM). Otago: Park Pass, 1200 m, 19 February 1968, *D. J. Galloway* s.n. (CHR 343384 p.p.), 1430 m, May 1968, *D. J. Galloway* s.n. (CHR 343380 p.p.); Humboldt Mountains, Mt. Amphion, above Park Pass, 1830 m, February 1971, *D. J. Galloway* s.n. (BM, CHR 343485); Humboldt Mountains, Mt. Nox (type locality); Sugar Loaf Saddle, 1070 m, May 1966, *D. J. Galloway* s.n. (CHR 343446 p.p.; BM, CHR 343413 p.p.). 1280 m, February 1968, *D. J. Galloway* s.n. (CHR 343408 p.p.); Forbes Mountains, western slopes, 1680 m, 2 December 1967, *A. F. Mark* s.n. (CHR 343462); Earnslaw Burn Valley, 1220 m, January 1968, *D. J. Galloway* s.n. (CHR 343362 p.p.); Wilkin Valley, Mt. Jumbo, 1830 m, January 1969, *A. F. Mark* s.n. (CHR 343385); Young Range, 1430 m, March 1968, *D. J. Galloway* s.n. (CHR 343436 p.p., CHR 343447 p.p.), 1520, March 1968, *R. J. Nilsson* s.n. (CHR 343396 p.p.); unnamed Virgin, N. of Pope's Nose, 2350 m, 11 February 1969, *L. D. Kennedy* s.n. (CHR 343366 p.p.); Mt. Roy, above Wanaka, 1 November 1972, *G. C. Bratt* 72/1506 (HO 35175 p.p.).

Uncertain determination

Otago: Mt. Ward, summit, 2590 m, January 1961, *R. G. Cunninghame* Murray 5629 (OTA).

11. **Usnea sphacelata** R. Br. **Figs 28–29**

Chloris melvilliana: 49 (1823 ['1821']). – *Usnea melaxantha* var. *sphacelata* (R. Br.) J. D. Hook., *Bot. Ant. Voyage 'Erebus & Terror'* **1**: *Flora Antarctica* **2**: 520 (1847). – *Usnea sulphurea* var. *sphacelata* (R. Br.) Vainio, *Ré. Voy. S. Y. Belgica, 1897–99, Botan., Lichens*: 11 (1903). Type: Melville I., *Mr James Ross* 114 (BM! – holotype; BM! – isotypes). [TLC: no medullary substances, usnic acid.] (see Note 1)

Lichen sulphureus J. König in Olafsen & Povelsen, *Reise igien. Island* Appendix: 16 (1772), non *Lichen suphureus* Retz. (1769) [Article 64.1]. – *Usnea sulphurea* Th. Fr. in *K. svenska VetenskAcad. Handl.* **7**(2): 9 (1867) [Article 72, note 1]. – *Neuropogon melaxanthus* f. *sulphurea* (Th. Fr.) Hue in *Nouv. Archs Mus. Hist. nat. Paris Ser. 3.* **2**: 272 (1890). – *Neuropogon sulphureus* (Th. Fr.) Hellbom in *Bih. K. svenska VetenskAkad. Handl.* **21** (3/13): 21 (1896). Type: Iceland (not extant). (see Note 2)

Lichen pallidus Retz., *Fl. Scandin. Prodrom.*: 234 (1779), non *Lichen pallidus* Schreber (1771). [Article 64.1]. Type: *Lichen sulphureus* J. König. (see Note 2)

Usnea frigida Dodge & G. Baker in *Ann. Mo. bot. Gdn* **25**: 603 (1938). Type: Marie Byrd Land, Edsel Ford Range, Mt. Rea-Cooper, *P. Siple, F. A. Wade, S. Corey & O. D. Stancliff* R1 (Herb. Dodge – holotype, not seen).

Neuropogon acromelanus var. *inactivus* f. *picatus* Lamb in *J. Linn. Soc.* (Bot.) **52**: 220 (1939). – *Usnea picata* (Lamb) Dodge in *Rep. B.A.N.Z. Antarctic Res. Exp.* **7**: 205 (1948). Type: [South Victoria Land] Cape Adare or Sastrugi, *Br. Antarct. 'Terra Nova' Exped. 1910* (BM! – holotype). [TLC: no medullary substances, usnic acid.]

Neuropogon acromelanus var. *inactivus* f. *scabridulus* Lamb in *J. Linn. Soc.* (Bot.) **52**: 220 (1939). – *Usnea scabridula* (Lamb) Dodge in *Rep. B.A.N.Z. Antarctic Res. Exp.* B **7**: 204 (1948). Type: Antarctica [unlocalised], *Campbell D. Mackellar* (BM! – holotype). [TLC: no medullary substances, usnic acid.]

Neuropogon ciliatus var. *subpolaris* Lamb in *J. Linn. Soc.* (Bot.) **52**: 217 (1939). – *Usnea subpolaris* (Lamb) Dodge, *Lich. Fl. Antarctic Cont.* 237 (1973). Type: South Victoria Land, Cape Sastrugi, Evans Cove, *Br. Antarct. 'Terra Nova' Exped. 1910* (BM! – holotype). [TLC: no medullary substances, usnic acid.]

Usnea laxissima Dodge in *Rep. B.A.N.Z. Antarctic Res. Exp.* B, **7**: 198 (1948). – *Neuropogon antarcticus* var. *laxissima* (Dodge) J. Murray in *Trans. R. Soc. N.Z.* (Bot.) **2**: 71 (1963). Type: Queen Mary Land, Possession Nunatak, 15 December 1912, *C. T. Harrisson*, AAE 84 (herb. Dodge – holotype, not seen; MEL 1012296! – isotype, CHR! – isotype). [TLC: no medullary substances, usnic acid (isotype).] (see Note 3)

Neuropogon lambii Imshaugh in *Rhodora* **56**: 154 (1954). Type: U.S.A., Washington, Mt. Rainier National Park, Yakima Park, 1830 m, 19 August 1942, *P. F. Scholander* (FH! – holotype). [TLC: no medullary substances, ± UV+ unknowns, usnic acid.]

?*Usnea striata* Zammuto in Dodge in *Trans. Am. micros. Soc.* **84**: 522 (1965). Type: Edward VII Peninsula, Rockefeller Mountains, Mt. Breckinridge, 78°03′S: 155°28′W, *R. G. Frazier & F. A. Wade* 315 (herb. Dodge – holotype, not seen). (see Note 4)

Note 1: *Usnea sphacelata* R. Br.

Type material is present in the BM. Material incorporated into collections bearing the species number and Brown's handwriting is recognised as holotype material (Fig. 28). This conforms with current research into Brown's bryophyte collections in BM (Harrington & Ellis, unpublished). Several isotypes are known, including boxed material of lichens and phanerogams forming 'Flora Antarctica' of Captain Parry's First Voyage. The name *Usnea sphacelata* was originally published by Brown (1823) in *Chloris Melvilliana* which was a preprint of his account in the Appendix to Capt Parry's Voyage (Brown, 1824) with independent pagination (Stafleu & Cowan, 1976); the 1824 reference has always been cited by previous authors (Zahlbruckner, 1930; Motyka, 1936; Lamb, 1939*a*).

Note 2: *Lichen sulphureus* J. König.

This name is a later homonym of *Lichen sulphureus* Retz. (Retzius, 1769) and is consequently invalid (Article 64.1). Retzius (1779) gave the taxon a new name, *Lichen pallidus*, but this is also invalid, being a later homonym of *Lichen pallidus* Schreber. The correct name for this taxon is consequently *Usnea sphacelata* R. Br.

Note 3: *Usnea laxissima* Dodge

Isotype material (Fig. 29) represents a weathered, decumbent form of *U. sphacelata*. Murray (1963) wrongly regarded this taxon to be a variety of *U. antarctica*, although a record from Macquarie Island (Filson, 1981) is probably referable to that species.

Note 4: *Usnea striata* Zammuto

This taxon is only known from the type collection from Edward VII Peninsula (Dodge, 1973) which has not been made available for study. The original description indicates that the taxon is synonymous with *U. sphacelata*.

Description: Thallus 1·5–5 cm, arising from a ± delimited or proliferating, rarely pigmented holdfast, erect, sparsely to richly branched above with capillaceous, attenuate branches. Fibrils usually absent. Branches terete, yellow-green, conspicuously variegated above with bands of black pigment or ± continuously pigmented violaceous black towards the apices. Cortex variable in thickness. Surface subnitid or matt, smooth to faveolate, rarely inflated, ± scabrid with minute, often pigmented papillae (×10 lens). Medulla lax or rarely sublax, axis thin, occupying 0·2–0·4 of the branch diameter. Soralia numerous, ± confined to ultimate branches, plane, emarginate, becoming convex-pulvinate to globose on maturity. Soredia granular, frequently partially corticate then pigmented. Pseudoisidia rare, isidia absent. Apothecia and pycnidia not seen. TLC: (1) psoromic acid, ± 2′-O-demethylpsoromic acid, usnic acid; (2) no medullary substances, ± 2–3 UV+ unknowns, usnic acid.

Distinguishing features: *Usnea sphacelata* is characterised by its erect, usually richly branched habit, a subnitid to subpapillate surface with prominent bands of pigment, a lax medulla, usually lacking depsidones, a thin axis, and plane to nodular, often pigmented, soralia more or less confined to secondary branches.

Distribution: *Usnea sphacelata* is the only known bipolar species of the subgenus. In the arctic its distribution is almost circumpolar including the New Siberian Islands in the east to Melville Island in the west. The species is known from Greenland, Iceland, Svalbard, Franz Joseph Land, Novaya Zemlya, Jan Mayen, and a few islands of arctic Canada, with its main distribution in the Canadian eastern arctic; it is rare in western arctic Canada. Its distribution has been adequately mapped by Lynge (1941) and Thompson (1972) and there are few recent additions. Figs 5 & 7.

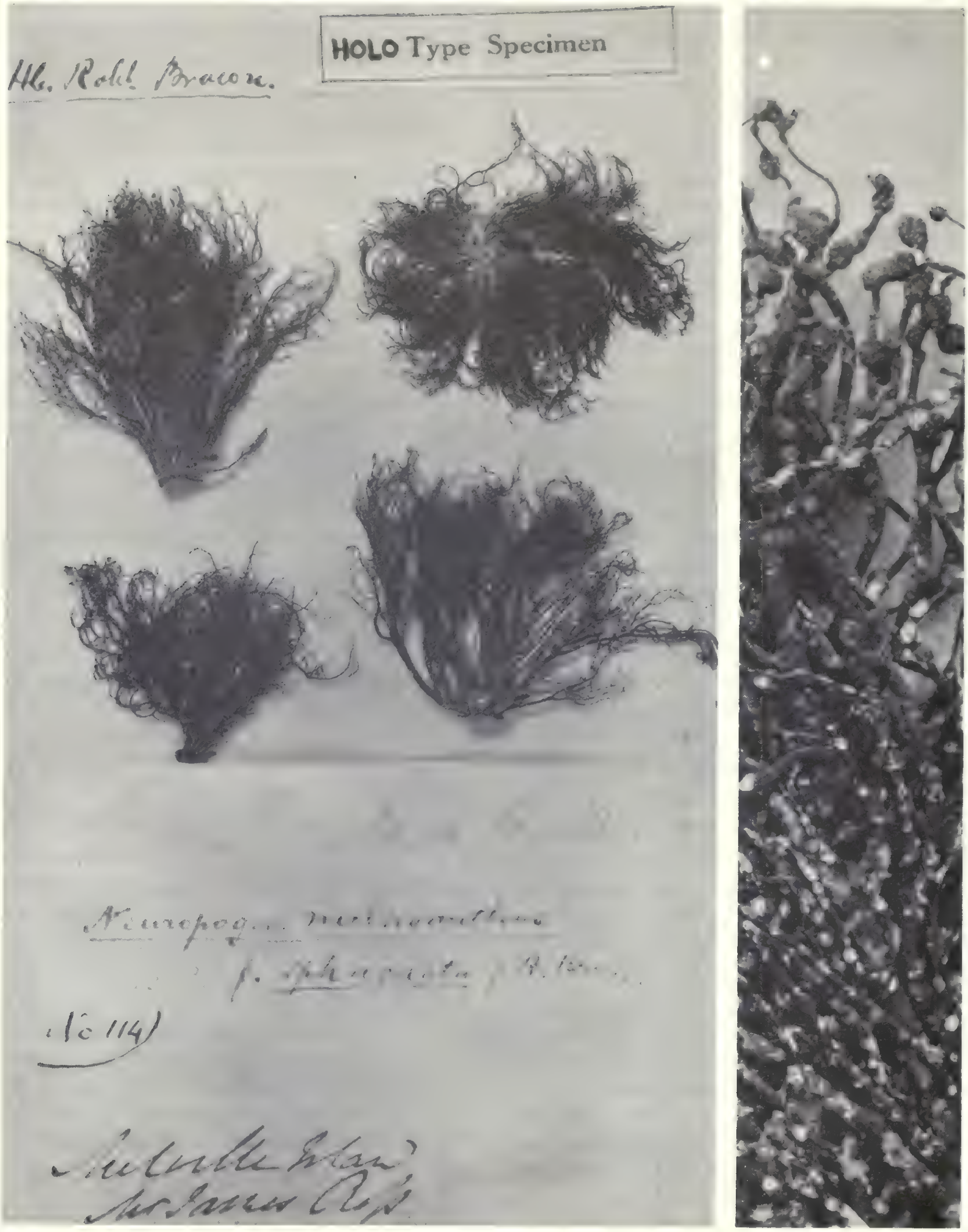


Fig. 28 Holotype of *Usnea sphacelata* R. Br. (BM) ×1. Inset. Detail of soralia ×10.

In Greenland *Usnea sphacelata* has a northerly distribution, although it is absent from the north coast. The species is frequent north of latitude *c.* 75°N on the east coast, rarely extending to latitude 68–70°N, and on the west coast as far south as Disko (Lynge, 1941; Lamb, 1939*b*). The species has only recently been discovered in southern Greenland (E. Hansen, 1982) at Nákâlâq (C!) slightly south of the area investigated by K. Hansen (1971) who failed to find the species.

In the arctic *Usnea sphacelata* is characteristically, but not obligately, an alpine species occurring, for example in Greenland, on the upper levels of rock falls and precipices (Lynge, 1932) and only occasionally at lower altitudes (K. Hansen, 1962). Towards the southern range of distribution in the arctic the species is confined to higher altitudes, and rarely occurs below 500–600 m in Iceland (Lynge, 1941) and western Svalbard (Lynge, 1941; Weber, *Lich. Exs.* 591); in the northern part of its range it occurs down to sea-level, for example in Franz Josef Land.

The species is very rare in the U.S.A., being only known from the type locality of *Usnea lambii* in Washington State and an additional record nearby (W. Weber, 1973). A single gathering from *c.* 4400 m in Mexico (Mt. Orizaba, *Metzger*, FH!, UPS!) forms a link between the North American distribution and that of the northern Andes.

In South America, *Usnea sphacelata* occurs in Ecuador at very high altitudes, and is very rare in Venezuela and Peru as far south as latitude *c.* 15°S. South of this latitude, apart from isolated, mainly high-alpine, subantarctic localities in New Zealand and Patagonia, there appears to be a significant gap in the distribution before the circumpolar antarctic populations are encountered. Many previous records from South America (as *U. sulphurea*) are erroneous and are referable to *U. patagonica, U. durietzii*, and *U. subantarctica*.

The species is absent, and is replaced by *Usnea antarctica*, from the Falkland Islands, South Orkney, and South Shetland Islands, as well as the South Sandwich Islands. On the antarctic continent *U. sphacelata* is circumpolar and is more frequent than *U. antarctica*, although occasionally misidentified as that species (for example, Follmann *Lich. Exs.* 399, BM!). As in the arctic it is frequently a species of high altitude, exposed locations, although also occurring at lower altitudes (see Bowra et al, 1966; Kashiwadani, 1970; Lindsay, 1972; Øvstedal, 1983). On the Antarctic peninsula the species occurs at a range of altitudes (Lamb, 1964) on the west coast, mainly south of the Antarctic Circle, and throughout the east coast, although it is often replaced at lower altitudes by *U. subantarctica* in the north-east and south-west.

Chemistry: Race 1, containing psoromic acid, is extremely rare and is only known from a single collection from the Andes in Peru tentatively assigned to this species. All other specimens examined were found to be depsidone-deficient; occasionally containing traces of UV+ unknowns. Specimens from Patagonia and the Antarctic peninsula containing norstictic and/or salazinic acids, previously referred to this species (Lamb, 1948*a*, 1964), belong to *Usnea subantarctica*, and, from the northern Andes, to *U. durietzii*.

Variation: Arctic populations of *Usnea sphacelata* are much more uniform than those from the southern hemisphere and are characterised, as found in the type specimen, by a richly branched, strikingly variegated thallus, with pigmented, nodular soralia. The thallus may arise from a delimited holdfast, although this is more frequently proliferating and spreading. Branching is more or less dichotomous and regular with the production of extended, variegated laterals which in turn may give rise to capillaceous, extensively pigmented, ultimate branches.

The thallus may be smooth to subfaveolate and is usually subnitid to waxy or rarely matt; it lacks pigmented annulations. Small, often pigmented, papillae are usually present; only rarely in a few arctic specimens are the main branches waxy, epapillate and unpigmented, as, for example, the type of *Usnea lambii*; the medulla is usually lax and arachnoid in main branches, but in some instances may not be fully expanded and then the axis occupies a greater proportion of the branch diameter.

Soralia are characteristically large, pulvinate, emarginate, sometimes geniculate; they tend to occur at intervals towards the apices of secondary branches, and are often broader than the subtending branch. Soredia often become partially corticate and pigmented but do not produce distinct pseudoisidia; they only lack black pigment when poorly developed as small punctiform soralia, or if the thallus is weathered or moribund.

In the northern Andes variation within populations is more diverse but is difficult to assess since the species appears to be rare. The 20 specimens examined are often extensively pigmented or lack several distinctive features of the species. Some thalli reflect the variation found in arctic populations. Others differ in having a delimited holdfast, are richly branches with extended laterals bearing minute, unpigmented, eroded soralia on a subnitid, subfaveolate to subpapillate thallus. Other variants resemble *Usnea acromelana* and are virtually monopodial, arise from a proliferating holdfast, and are infrequently branched with large, pale, excavate soralia; however, they may be distinguished by a lax or sublax medulla and absence of annulations. Rarely the medulla may become markedly inflated or small pseudoisidia are produced, thus superficially resembling *U. durietzii*. Occasionally thalli, tentatively referred to this species, are found in collections of *U. durietzii*; these are extensively pigmented and papillate, and have plane soralia and a compact medulla (for example, *Arvidsson & Nilson* 945 p.p., GB!).

Material conforming to arctic populations is still present, but less frequent, in the antarctic regions and appears to be confined to lower altitudes where it is often replaced by *Usnea subantarctica* in areas where their distributions overlap. In such instances the two species may be separated by the way in which secondary branches are produced and sometimes by their medullary chemistry. Material described as fertile *U. sulphurea* (Lindsay, 1969) is referable to *U. subantarctica* (p. 102).

Thalli of *Usnea sphacelata* from Antarctica, particularly from high altitudes, are erect or rarely subdecumbent and are often more or less monopodial arising from a proliferating holdfast, occasionally branching extensively towards the apices. Rarely in subdecumbent thalli, are the secondary branches extensive, divergent and capillaceous with flexuose apices; producing a fragile, interwoven network which resembles, but is not as extensive as, that of *Usnea subcapillaris* and *U. pseudocapillaris* (for example, Dronning Maud Land, H. U. Sverdrupfjella, *Angard,* TROM!). Pigmentation is confined to apices and tends to be continuous rather than variegated and is violaceous black. The cortex is often thicker and the surface subnitid, sometimes epapillate, rarely faveolate and fracturing, whilst the medulla may only be sublax. Consequently such thalli have sometimes been mistaken for species of the *U. ciliata* complex (Lamb, 1939*a*, 1948*a*; Dodge, 1973; Murray, 1963) and described as distinct taxa; *Neuropogon ciliatus* var. *subpolaris* is a sparsely sorediate, decumbent form of *U. sphacelata* whilst in *N. acromelanus* var. *inactivus* f. *picatus* and f. *scabridulus* the medulla is only lax towards the axis and weathering of the thallus has given rise to development of untypical annulations.

Specimens from New Zealand and Patagonia resemble those antarctic populations that bear a superficial resemblance to *Usnea acromelana*. In these the medulla may only be slightly lax, the surface epapillate, and the soralia small, plane and unpigmented. In New Zealand the two species may easily be distinguished by differences in medullary chemistry, whilst in Patagonia and the Antarctic peninsula more critical examination of morphological features is required.

Species concept: Although the range of variation of antarctic populations of *Usnea sphacelata* is much greater than that in the arctic, I do not consider this sufficient for the recognition of separate taxa. In addition thalli resembling the type from the arctic are also present in Antarctica, as well as a range of intermediate forms. The only distinction that has been made here is the recognition of a new species, *U. subantarctica* (p. 99), which is characterised by a more open branched habit with dispersed fibrils, often forming tassel-like apices; in contrast *U. sphacelata* has fewer, broader, extended laterals, usually lacking fibrils, and lacking a norstictic acid-containing race.

Dodge & Baker (1938) only recognised *Usnea sphacelata* from Patagonia northwards, whilst Dodge later (1973) referred to this as solely an arctic species, describing most continental antarctic material as a distinct species, *U. frigida*, in addition to his other taxa that are here also regarded as synonyms. From the original description and illustrations (Dodge & Baker, 1948), and from Lamb's subsequent report (Lamb, 1964) on a prepared slide of the holotype of *U. frigida* and his examination of material from the type locality ex MO, (Lamb, unpublished notes, AAS!) it is clear that this taxon is a synonym of *U. sphacelata*. In addition specimens examined from a nearby locality (KASSEL 24772, ex herb. Dodge!) and material distributed by OS as *U. frigida* (BM!, CANL!, KASSEL!) though depauperate, are also clearly referable to this species.

Some thalli of *Usnea sphacelata* bear a superficial resemblance to those of *Usnea acromelana*, particularly from New Zealand and Patagonia. This might suggest either a parallel evolution of characters from a common ancestry or, remotely, some indication of hybridisation between the

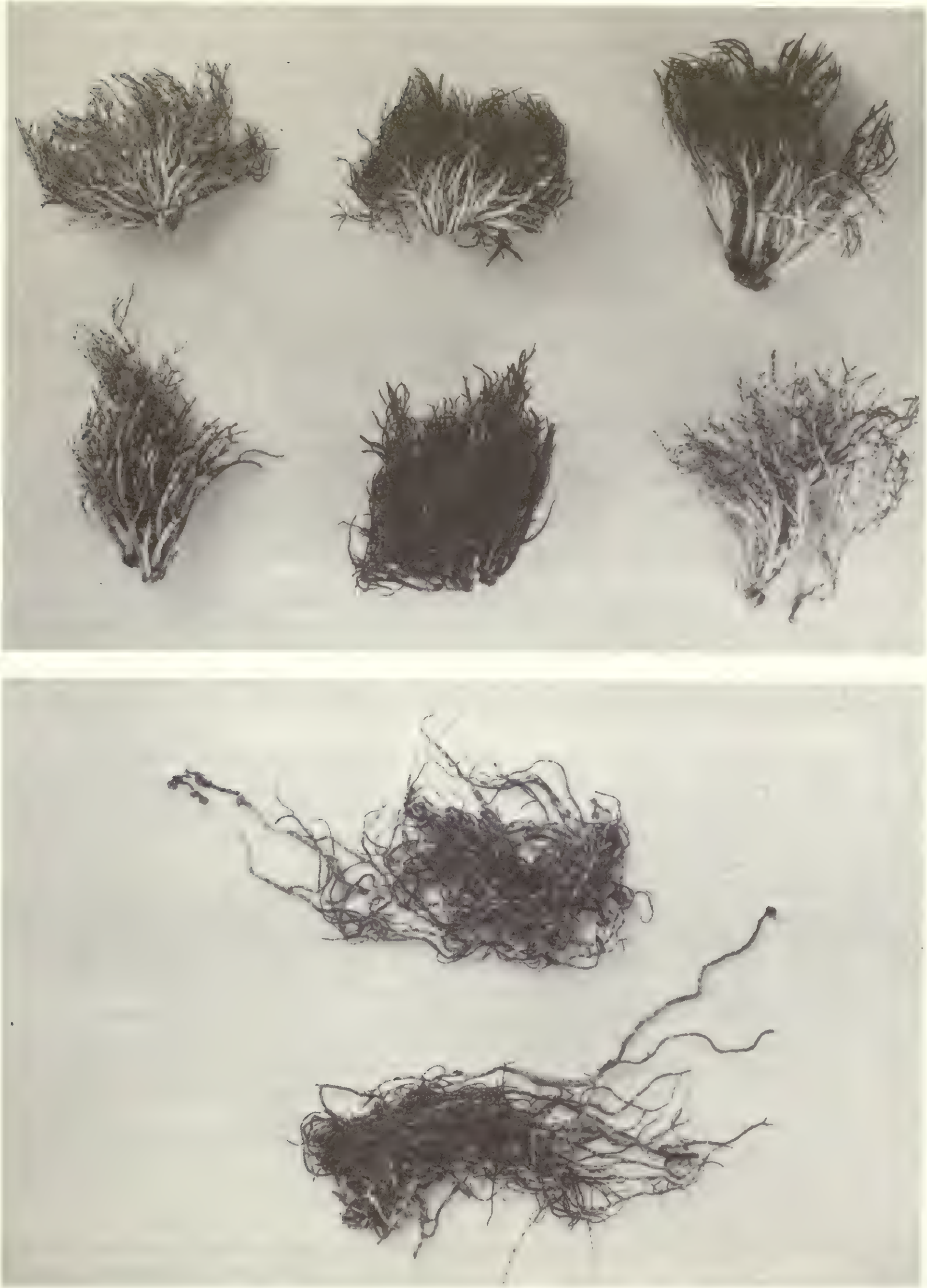


Fig. 29 *Usnea sphacelata*. Variation in southern hemisphere populations. Top. New Zealand, Otago, Mt. Aspiring, *Kennedy* (CHR 343354) ×1. Bottom. Isotype of *Usnea laxissima* Dodge (MEL 1012296) ×1·5.

two species. However, on evidence, it is more likely that *U. sphacelata* has closest affinities with *U. perpusilla*. Features common to *U. sphacelata* and *U. perpusilla* include a diverse range of habit and similar branching, pigmentation, surface ornamentation, variation in medulla width, and lack of chemistry.

Occasionally thalli are encountered that are somewhat intermediate between *Usnea sphacelata* and *U. antarctica* (see synonymy in both species), but these similarities are superficial and are most likely to occur in immature specimens. Close examination reveals the characteristic anatomical, surface, and soralia features of the two species. The soralia of *U. sphacelata* tend to be more globose than in *U. antarctica* and lack the distinctive crateriform margin, and are less widely distributed throughout the thallus. The species may be distinguished from *U. subantarctica* by differences in branching and papillation; from *U. acromelana* by a laxer arachnoid medulla and lack of pigmented annulations; from *U. durietzii* and *U. patagonica* by the absence of pseudoisidia; from *U. acanthella* by the absence of true isidia.

Selected specimens examined
Race 1
PERU. Puno: San Antonio de Esquilache [16°08′S: 70°22′W], 4750 m, 20 May 1937, *D. Stafford* 762 (BM, FH).
Race 2
JAN MAYEN. [71°00′N: 9°00′W], Eskkrateret, 22 July 1930, *J. Lid* s.n. (BM).
ICELAND. Syðri Bjarghóll [*c.* 65°40′N: 16°45′W], 8 km NE. of Reykjahlið, Suður Þingeyjarsýsla, *c.* 550 m, 11 August 1982, *C. D. & D. H. Dalby* s.n. (BM); Nordur-Múlasýsla, Austurfjallgardur, Mödrudalsörafi [65°20′N: 15°42′W], 680 m, 10 July 1979, *H. Hertel* 21586 (M); Ytri Baegisá, Akureyki [65°41′N: 18°04′W], 610 m, August 1963, *B. A. Rowland* L17 (BM); Tungnafjellsjökull [64°45′N: 17°55′W], 1300 m, 8 August 1967, *H. Kristinsson* 23095 Vězda: Lich. Sel. Exs. 886 (BM); Kjallfell, 26 July 1895, *Stefansson* s.n. (C).
GREENLAND. Disko I.: Lyngmarksfjeldt [69°16′N: 53°35′W], 200 m, 16 July 1974, *P. Mellergård & E. S. Hansen* s.n. Lich. Groen. Exs. C 102 (BM, C, M), head of Nordfjord [67°57′N: 54°19′W], 26 June 1952, *P. Gelting* Lich. Groen. Exs. C 152 (BM, C, M); Svartenhuk, Simiutaq [71°53′N: 52°25′W], 1200 m, August 1949, *N. Berg* s.n. (C); Angmagssalik district, S. of Pourquoi-Pass glacier [66°39′N: 35°40′W], 1500 m, 8 August 1966, *M. Zumbühl* s.n. (C); Nákâlâq [60°59′N: 45°55′W], 1400 m, 20 August 1975, *D. Olsen* L-1405 (C).
CANADA. North West Territories: Ellesmere Land, North Kent I. [76°30′N: 90°00′W], 13 July 1901, *Simmons* s.n. (BM); Franklin district, Bathurst I., E. side of May Inlet, N. of Purcell Bay [76°23′N: 100°47′W], *c.* 25 m, 9 July 1963, *Weston Blake* 19a (C, UPS); Parry Is., Melville I [*c.* 75°N: 112°W] (type locality *U. sphacelata*) *J. Ross* s.n. (BM).
NOVAYA ZEMLYA [74°40′S; *c.* 55°E]. see Lynge (1941).
NEW SIBERIAN IS. [*c.* 76°N: 140°E]. see Lynge (1941).
FRANZ JOSEF LAND. Hooker I. [81°S: 53°E], Ssedov ‘promitory’, 1930, *V. P. Savicz* Savicz: Lich. Rossica (5) 43 (M), [Northbrook I.] Cape Flora, 1901, *Palibin* s.n. Elenkin: Lich. Flor. Rossiae 113a (BM, FH, US).
SVALBARD. Spitzbergen: Isfjord area, near Longyearbyen [78°12′N: 15°40′E], Mt. Nordenskjold, 100 m, 3 August 1975, *H. Hertel & H. Ullrich* s.n. Lich. Exs. COLO 591 (BM, C, M); Svalhardhytta, *c.* 200 m, *A. Hoeg & J. Lid* s.n. Krypt. Exs. Vindobon. 3070 (BM, C, M, WU 2886); Wahlenbergsbay (Hinlopen Strait), 1861, *A. J. Malmgren* s.n. Fries. Lich. Scand. Exs. 51 (BM, M); Brandewijnsbay, 150 m, *O. Torrell* s.n. Zahlbr.-Redinger, Lich. Rar. Exs. 384 (BM, WU3085).
UNITED STATES. Washington: (type locality of *Neuropogon lambii*).
MEXICO. Veracruz: SE. of Mt. Orizaba [18°51′N: 97°08′W], Citlaltepetl, 4330–4540 m, 17 August 1966, *U. V. Metzger* s.n. (FH, UPS).
VENEZUELA. Merida: paramo de Campanario, 4000 m, 19 September 1938, *J. Hanbury-Tracy* 168 (BM). Barinas: Pico de las Piedras Blancas, 4762 m, 25 May 1952, *V. Vareschi* 1259 p.p. (US).
COLUMBIA. Caldas: Nevado del Ruiz, NW. side, *c.* 1500 m, 3 February 1979, *H. Sipman & H. Valencia* 10423 (BM, U).
ECUADOR. Pichincha: Quito, Pinchincha, crater margin, 30 June 1939, *E. Asplund* s.n. Lich. austroam. ex herb. Regnelliano 360 (BM, C, H, LD); E. slopes Cerro Iliniza, *c.* 4400 m, 7 March 1972, *L. Arvidsson & D. Nilson* 945 p.p. (GB); summit of Corazón, 4861 m, *E. Whymper* 1323 (10) (BM). Napo: Antisana, 4900 m, *E. Whymper* 1329 (2) (BM). Bolivar: W. side of Chimborazo, 4780 m, 1967, *Cambridge Lichen Exped.* s.n. (BM). Chimborazo: NW. face of Chimborazo, 3700–4300 m, January 1859, *Wagner* s.n. (M).
ARGENTINA. Santa Cruz: Patagonia, Lago Viedma, Volcan nunatak, *c.* 13 km from nearest land in Hielo Continental, January 1959, *G. Bratt* s.n. (BM).
ANTARCTIC PENINSULA. Graham Land: Joinville I. [63°18′S: 57°56′W], N. end of Active Sound, 200 m, 27 March 1981, *R. I. L. Smith* 3736 p.p. (AAS), Crown Prince Gustav Channel, Alectoria I. [63°59′S:

58°37′W], 30–60 m, 18 August 1945, *I. M. Lamb* Operation Tabarin 2465 (BM), Nordenskjold coast [*c.* 64°30′S: 59°00′W], nunatak 6·4 km NW. of head of Larsen Inlet, *c.* 910 m, 23 September 1960, *C. G. Brading* 105a (AAS), Oscar II coast, N. side of Churchill Peninsula [*c.* 66°30′S: 62°50′W], 460 m, November 1963, *R. Tindall* 18 (AAS), Foyn coast, Cape Robinson [*c.* 67°S: 64°W], E. of Mt. Hayes, 6 October 1964, *G. Stubbs* B.A.S. Misc. 6 (AAS), Fallières coast, Adelaide I. [*c.* 67°15′S: 68°30′W], 'Reptile Ridge', Yellow Bluff, 350 m, 9 March 1981, *R. I. L. Smith* 3453 p.p. (AAS). Palmer Land: Wilkins coast [69°20′S: 63°41′W], 1070 m, 23 October 1965, *M. J. Cousins* 22 (AAS), Alexander I., Ablation Valley [70°48′S: 68°30′W], *c.* 5 m, January 1979, *D. England* 2692 (AAS), Alexander I., Two-Step Cliffs [71°51′S: 68°17′W], *c.* 600 m, 4 February 1979, *D. England* 2688 (AAS), Black coast, Cape Bryant area [72°19′S: 60°40′W], 45 m, 23 January 1948, *K. S. P. Butler & B. Stonehouse* F.I.D.S. E1228 (BM), George VI Sound, Eklund Is. [73°20′S: 72°00′W], 20 November 1949, *V. E. Fuchs* et al. F.I.D.S. E604 (BM, FH).

DRONNING MAUD LAND. [*c.* 15°W]. H. U. Sverdrupfjella, Jutulrøra [*c.* 20°W], 1500 m, 11 December 1970, *J. Angard* s.n. (BG), Vestfjella [*c.* 13–16°W], Müren, 21 January 1977, *L. Sømme* 204(102) (BG, BM).

ELLSWORTH LAND. [*c.* 72–74°W]. Johnson nunatak, survey point, 7 January 1962, *J. T. R. Molholm* 6 (BM, CANL 21331, KASSEL 26669), Barnes nunatak, *c.* 1560 m, 9 January 1962, *J. T. R. Molholm* 10 (AAS).

MARIE BYRD LAND. Edsel Ford mountains [*c.* 145°W], peak 1207, 9 December 1940, *H. P. Gilmour* U.S.A.S. 234 (US) (type locality of *Usnea frigida* Dodge & G. Baker), Mt. Grace McKinley [*c.* 148°W], 1934, *Second Byrd Exped.* (KASSEL 24772).

EDWARD VII LAND. [*c.* 150°W]. Rockefeller Mountains, Mt. Paterson, 18 December 1940, *R. G. Fitzsimmons* U.S.A.S. 278 (US), Mt. Breckenridge, 14 December 1940, *R. G. Frazier & F. A. Wade* U.S.A.S. 312 (US).

VICTORIA LAND. [*c.* 165°E]. Yule Bay, Birthday Ridge, 17 December 1981, *L. Kappen* 3001 (KIEL), Follmann: Lich. Exs. 399 (BM), Hallett Peninsula, 10 January 1963, *J. Cranfield* 7 (BM).

KNOX COAST. (*c.* 110°E). Bailey Peninsula, near Casey Station transmitter building, 35 m, 13 December 1982, *R. D. Seppelt* 13103 (herb. Seppelt).

QUEEN MARY LAND [*c.* 98°E]. Hippo nunatak, 29 December 1912, *C. T. Harrisson* s.n. A.A.E. 71-2 (AD), A.A.E. 71-3 (AD).

MAC.ROBERTSON LAND. [*c.* 70°E]. Falla Bluff, 9 February 1974, *R. Filson* 14910 Lich. Ant. Exs. 22 (AAS, BM, M, O).

ENDERBY LAND. [*c.* 50°E]. 3 March 1961, *E. Korotkevish* 70 (AAS), 1961, *G. Konovalov* 72 (FH).

PRINCE OLAV COAST. [*c.* 44°E]. Molodyozhnaya, *c.* 40 m, 8 February 1968, *H. Kashiwadani* J.A.R.E. 4118 (FH, H).

SOYA COAST. [*c.* 39°E]. *c.* 20 m, 12 January 1968, *H. Kashiwadani* J.A.R.E. 3823 (H), J.A.R.E. 3773 (H).

NEW ZEALAND. Nelson: Cobb Valley, *c.* 1490 m, 18 December 1982, *J. K. Bartlett* 25810 (herb. Bartlett, BM). Otago: Mt. Aspiring, NE. to Coxcomb Ridge, 2790–2850 m, 13 February 1969, *L. D. Kennedy* s.n. (CHR 343354), 2290 m, January 1957, *B. J. Wilkins* s.n. Murray 1040 (OTA), NW. Ridge, 2590 m, 27 January 1969, *D. J. Galloway* s.n. (CHR 342745); Pope's Nose, NE. Ridge, 2650 m, 8 February 1969, *L. D. Kennedy* s.n. (CHR 343319); Mt. Sir William, 2560 m, 27 December 1970, *D. J. Galloway* s.n. p.p. (CHR 342781 p.p.); Matukituki Valley, Mt. Avalanche, 2560–2590 m, 15 February 1969, *L. D. Kennedy* s.n. p.p. (CHR 343358 p.p.).

The following may be consulted for further localities: arctic regions (Lynge, 1941; Thomson, 1972), Antarctic peninsula (Lamb, 1964) (excluding specimens here referred to *Usnea subantarctica*), continental Antarctica (Bowra et al., 1966; Dodge, 1973; Kashiwadani, 1970; Lindsay, 1972; Øvestedal, 1978); lists held in BM and collections in AAS and BM.

12. **Usnea subantarctica** F. J. Walker, **sp. nov.** **Figs 30–31**

Diagnosis: Thallus fruticosus, pigmento nigro in cortice ad apices basimque conspicue coloratus. Rami irregulares teretes fibrillosi, papillis numerosis nigriscentibus. Medulla laxa vel sublaxa. Soralia convexa vel nodulosa nigrescentia. Apothecia rara disco rufescenti, apotheciis Usneae trachycarpae similia. Acidum usnicum et acidum norstictum continens. Typus: Antarctic peninsula: Western shore of bay east of old base, on west, coast of Horseshoe I., Marguerite Bay, Fallières Coast, 7·5 m, 23 February 1965, *R. E. Longton* 1275 (AAS! – holotype; BM! – isotype). [TLC: norstictic acid, ± UV+ unknowns, usnic acid.]

Description: Thallus 1·5–3·5 cm, arising from a proliferating, rarely pigmented, holdfast, erect or rarely subdecumbent, moderately branched above with short, ± divergent, flexuose, attenuate secondary branches. Fibrils ± extensive, irregularly dispersed, to give an open, spinulose to tassel-like habit. Branches terete, yellow-green, ± continuously black pigmented towards the apices or variegated with bands of pigment. Cortex thin. Surface matt, conspicuously scabrid with small, pigmented papillae. Medulla lax or sublax, axis thin, occupying 0·3–0·5 of the branch diameter. Soralia numerous, ± confined to ultimate branches, plane becoming convex to pulvinate or nodular, rarely marginate. Soredia granular, often partially corticate then pigmented. Pseudoisidia rare, isidia absent. Apothecia rare, as in *U. trachycarpa*. Pycnidia not seen. TLC: (1) norstictic acid, salazinic acid, usnic, acid; (2) no medullary substances, usnic acid.

Distinguishing features: *Usnea subantarctica* is characterised by its erect, spreading, richly branched, irregular habit, a matt, papillate, a more or less extensively pigmented surface, a lax or sublax medulla, often containing norstictic and/or salazinic acids, and nodular, often pigmented, soralia more or less confined to secondary branches.

Distribution: *Usnea subantarctica* has a distribution similar to that of *U. aurantiaco-atra*, although it is largely restricted to the Antarctic peninsula; it is rare in southern South America. The species is absent from continental Antarctica and the islands of the Scotia Arc, but may eventually be found elsewhere in the subantarctic regions.

On the Antarctic peninsula the distribution is similar to that of *Usnea sphacelata*, being more frequent on the north-east coast and at lower latitudes on the west coast. The species has been found in association with *U. aurantiaco-atra, U. acromelana,* and *U. antarctica* (*R. I. L. Smith* 3680, AAS!) and also with *U. antarctica* and *U. sphacelata* (*R. I. L. Smith* 3736, AAS!). In this area the species is usually confined to lower altitudes, frequently replacing *U. sphacelata*, and is rarely found above *c.* 500 m where *U. sphacelata* predominates. Its ecological requirements appear to be somewhat intermediate between those of *U. antarctica* and *U. sphacelata*. The majority of specimens on which Lamb (1964) based his distribution map of depsidone-containing material of *U. sphacelata* (as *U. sulphurea*) have been examined and are referable to this species as well as some depsidone-deficient material. *Usnea subantarctica* is less frequent in Patagonia, often being replaced by other asexual species, including *U. patagonica*, and is there confined to higher altitudes in the alpine region of the Andes, mainly between 1000–2000 m, where it has been collected with *U. antarctica* and *U. trachycarpa*. Fig. 5.

Chemistry: Two chemical races have been detected in *Usnea subantarctica*. The dominant race contains norstictic acid (Race 1) with occasional traces of salazinic or connorstictic acids or rarely just salazinic acid, whilst the other (Race 2) is depsidone-deficient. UV+ unknowns may occur, but are rare and only present in low concentrations. Similarly traces of unidentified fatty acids have also been detected, but these are not a constant feature as in *U. trachycarpa* or *U. patagonica* and hence do not have taxonomic significance. Both races have similar distributions and are of approximately the same frequency; however, the presence of norstictic acid does appear to be of salient importance in circumscribing the species.

Variation: *Usnea subantarctica* is usually characterised by an irregular habit that is reminiscent of an 'untidy' specimen of *U. sphacelata*, but usually has more fibrils, especially towards the apices giving a tassel-like appearance. Indeed, immature, small thalli of the two species, particularly from the Antarctic peninsula, may be indistinguishable on morphological characters, although chemical and ecological data may assist in identification.

Thalli may be sparingly branched, with extensive, small, blackened papillae, or may be richly branched and possess fibrils. Secondary branches are produced irregularly along the main axis, giving an open, spreading, divergent, habit; only infrequently may main branches remain in a close cluster or are richly branched from the base, as found in some forms of *Usnea sphacelata*. Rarely thalli may resemble northern hemisphere forms of *U. sphacelata* but are usually more irregularly branched with fibrils.

Variation in surface ornamentation and branch anatomy is similar to that of *Usnea trachycarpa*, and much of the discussion of that species is referable here (p. 113). However, some differences do occur: pigmentation is often more extensive, occasionally resulting in prominent

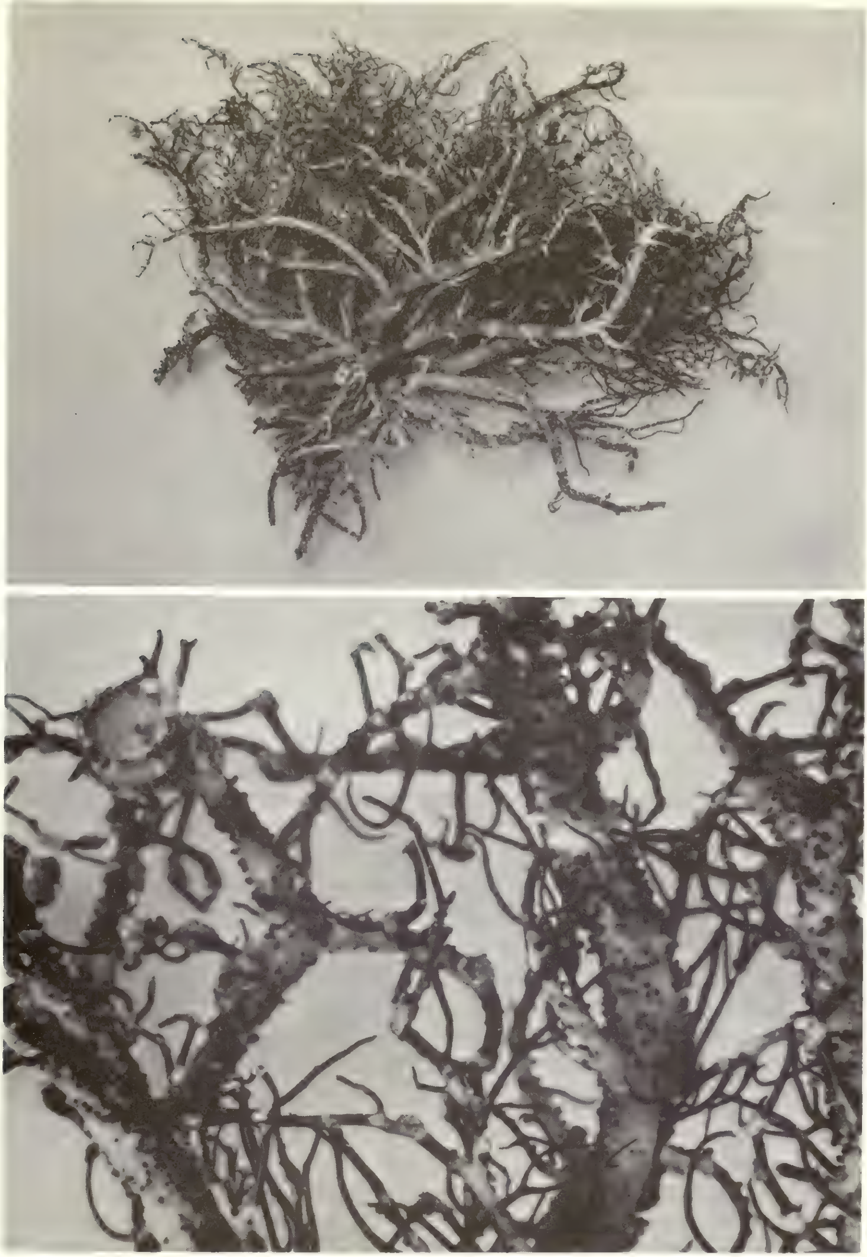


Fig. 30 Holotype of *Usnea subantarctica* F. J. Walker (AAS). Top. Whole thallus ×1. Bottom. Detail of apothecium and soralia ×10.

variegation, even of the fibrils; papillae on primary branches may less frequently give rise to fibrils; the surface is rarely faveolate or subnitid, although may occasionally fracture due to collapse of the underlying lax medulla.

Soralia are more or less confined to branch apices or secondary branches and are usually convex to globose, often pigmented, well spaced and wider than the subtending branch, and are similar to some forms of *Usnea sphacelata*, particularly from the arctic. Soralia production tends to foreshorten the ultimate branches (cf. *U. patagonica*) often resulting in flexuose geniculation of the branch. Soralia appear to arise directly from the cortex, by localised breakdown, and are not usually derived from papillae, although occasionally a surrounding margin, similar to that of *U. patagonica* or *U. antarctica*, is produced in instances where cortical papillae are particularly numerous and prominent.

Apothecia are rare and are identical to those of *Usnea trachycarpa*. They are only known from the holotype where they are immature, and an additional collection (Fig. 31) in which they are well-developed (*R. I. L. Smith* 829, AAS!). The fruits of the latter specimen were described by Lindsay (1969) and ascribed to *Usnea sulphurea*.

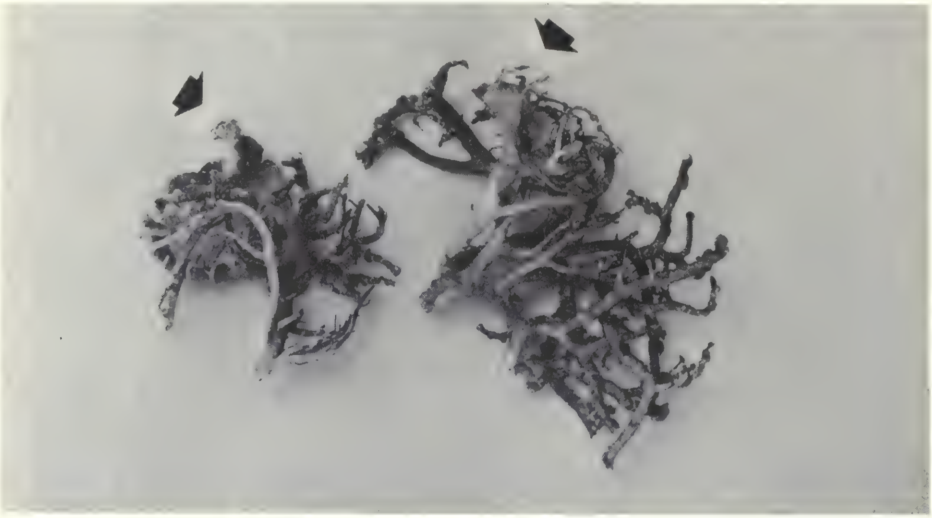


Fig. 31 Fertile thalli of *Usnea subantarctica*. Antarctic peninsula, Horseshoe I., *Smith* 829 (AAS) ×1·5.

Some specimens from Patagonia are more variable and, because of the range and variation of species found, may require more critical examination and are only tentatively included under this species. Others tend to have more conspicuous, stouter, spreading fibrils. Specimens tentatively referred to this species include one cited by Lamb (1948*a*), as *Usnea sulphurea*, from Sierra Alvear, Tierra del Fuego (*Santesson* 640e, S!), containing norstictic acid, and a depsidone-deficient thallus from a nearby locality (*Santesson* 641c, S!) mixed with *U. antarctica*. These show some similarities to papillate forms of *U. perpusilla*, which might indicate affinities with *U. sphacelata*, since they have fewer fibrils and have less prominent papillae.

Species concept: Although morphologically very similar to *Usnea sphacelata, U. subantarctica* is regarded as a distinct species, by virtue of differences in habit and branching, the presence of prominent fibrils and papillae, and apothecia that are identical to those of *U. trachycarpa*. Differences between the two species have been discussed above and also under *U. sphacelata* (p. 96). It might be argued that some specimens of *U. subantarctica* are very similar to some northern hemisphere forms of *U. sphacelata*. However, arctic forms of the latter species have extended laterals rather than short, undivided fibrils and lack the short, spreading, attenuate fibrils on primary branches.

Despite the lack of fertile material it is tentatively proposed (p. 40) that *Usnea sphacelata* is the sorediate counterpart of *U. perpusilla* and consequently would be expected to have a black rather than rufous brown apothecial disc. Consequently it appears that *U. subantarctica* has a closer relationship to *U. trachycarpa* than to *U. sphacelata–U. perpusilla*. This supposition is enhanced by the presence of norstictic acid in a significant proportion (*c*. 60%) of the specimens. However, a number of depsidone deficient gatherings are only tentatively referred to this species. If there were excluded the incidence of Race 1 would be 70%. Although traces of fatty acids have been detected in *U. subantarctica*, it is not certain that these have affinities with the murolic acid complex of *U. trachycarpa*. For this reason there must remain some doubt as to whether these taxa represent a species pair. However, specimens are often very similar to high-alpine forms of *U. trachycarpa*, originally described as f. *elatior* by Lamb (1948*a*), from Patagonia which are extensively pigmented and have scattered, short, attenuate fibrils and frequently lack medullary substances and fatty acids. The absence of fatty acids might be the consequence of more exposed habitats and this would explain their absence from *U. subantarctica*, particularly in the Antarctic peninsula.

It is evident from study of the synonymy of *Usnea sphacelata* that there is no existing name for the new species. Furthermore, existing names under *U. sphacelata* refer to material from continental Antarctica, outside the distributional range of *U. subantarctica*.

The epithet *'subantarctica'* is selected to refer to the distribution of the species, which although limited, does extend into the subantarctic area. It is likely that the species may eventually be found to be more widespread. A possible relationship to alpine forms of *Usnea trachycarpa* is also indicated, since that species also has a characteristic, albeit wider, distribution in the subantarctic. The distribution may eventually be compared to that of generally accepted species pairs, for example *U. ciliata–U. acromelana* and *U. aurantiaco-atra–U. antarctica*, in which the asexual species extends further south than the fertile counterpart.

Usnea subantarctica may be separated from other asexual species of *Neuropogon* by its untidy to tassel-like appearance and close resemblance to some forms of *U. trachycarpa*. The form of the soralium may resemble some variants of *U. sphacelata* and *U. acromelana* or may sometimes be marginate, although this is as non distinct as the plane, crateriform soralium of *U. antarctica*. The lack of distinct pseudoisidia separate the species from *U. durietzii* and *U. patagonica* whilst the lax medulla and the matt, surace with papillae and fibrils distinguish the species from *U. acromelana*.

Specimens examined

Race 1

CHILE. Aisén: Lago San Martin [49°S], 1600 m, 2 February 1933, *A. Donat* 3 p.p. (H).

ARGENTINA. Santa Cruz: Peninsula Magallanes, near Puerto Bandera, *c.* 1000 m, December 1958, *P. W. James* 59 p.p. (BM); Rio Fosiles, *c.* 1000 m, April 1905, *P. Dusén* s.n. p.p. (H).

ANTARCTIC PENINSULA. Graham Land: Joinville I. [63°18'S: 55°48'W], Mt. Alexander, 200–500 m, 27 March 1981, *R. I. L. Smith* 3680 p.p. (AAS); Trinity Peninsula, Duse Bay [63°48'S: 57°17'W], NE. of unnamed nunatak, [63°36'S: 57°01'W], 385 m, 27 March 1946, *J. D. Andrew* F.I.D.S. D109-6 p.p. (BM), Bald Head, 60–150 m, 18 November 1945, *I. M. Lamb* Operation Tabarin 2801 p.p. (BM), Duse Bay, [63°33'S: 57°22'W], 13 November 1945, *G. Davies* F.I.D.S. D2632 (BM, FH), Duse Bay, View Point [63°36'S: 57°01'W], *c.* 15 m, 10 November 1945, *I. M. Lamb* F.I.D.S. D2622 (BM), Crown Prince Gustav Channel, Beak I. [63°37'S: 57°20'W], *c.* 9 m, 28 December 1945, *I. M. Lamb* F.I.D.S. D2712 (BM), Egg I. [63°41'S: 57°42'W], 120 m, 11 November 1945, *I. M. Lamb* F.I.D.S. D2756 (+ Race 2) (BM), Pitt Point [*c.* 63°S: 58°W], *c.* 30 m, 17 August 1945, *I. M. Lamb* Operation Tabarin 2448 (BM), Operation Tabarin 2452 p.p. (BM), Operation Tabarin 2454 p.p. (BM), Operation Tabarin 2456 p.p. (BM), Church Point, [63°41'S: 57°54'W], 75 m, 10 December 1946, *J. D. Andrew* F.I.D.S. D114-2 (BM), F.I.D.S. D114-3 (BM), foot of East Russell Glacier, [63°44'S: 58°17'W], 550 m, 14 December 1946, *A. Reece* F.I.D.S. D369-8a (BM), 'Mt. Fitzroy' [63°48'S: 58°29'W], 240 m, 19 December 1946, *A. Reece* F.I.D.S. D37 (BM), Vega I. [63°50'S: 57°25'W], False Island Point, 6–18 m, 5 December 1945, *I. M. Lamb* Operation Tabarin 2724 (BM), D2722 (BM), Tabarin I. [63°52'S: 57°00'W], 150 m, 6 January 1946, *E. H. Back* Operation Tabarin 2852 (BM); James Ross I. [63°47'S: 57°47'W], Cape Lachman, *c.* 30 m, 21 November 1945, *I. M. Lamb* F.I.D.S. D2677 (BM p.p., CANL 17256), F.I.D.S. D2778 (BM), James Ross I., the Naze, 6–22·5 m, 26 November 1945, *I. M. Lamb* Operation Tabarin 2789 p.p. (+ Race 2) (BM); Palmer Archipelago, Wiencke I. [64°49'S: 63°22'W], E. of Wall Range, 370 m, 8 October 1944, *I. M. Lamb* F.I.D.S. A1323 (BM); Fallières Coast, Adelaide I. [67°15'S: 68°30'W], 'Stork' nunatak, 550 m, 9 March 1981, *R. I. L. Smith* 3416 (AAS); Fallières Coast, Marguerite Bay, Bourgeois Fjord [67°40'S: 67°05'W], 15 December 1936, B.G.L.E. 1518-3 (BM), Ridge I. [67°42'S: 67°06'W], 4 August 1936, B.G.L.E. 1484-3 (BM), Jenny I. [67°44'S: 68°25'W], E. coast, 15 m, 30 January 1961, *B. J. Taylor* 444b (AAS), Horseshoe I. [67°51'S: 67°12'W], (type locality), 7·5 m, 23 February 1965, *R. E. Longton* 1275 (BM), 24 February 1967, *R. I. L. Smith* 829 (fertile) (AAS), 6–10 m, 22 February 1977, *R. I. L. Smith* 2165 (AAS), between Lystad Bay and former B.A.S. station, 20–30 m, 22 February 1977, *R.I.L. Smith* 2168 (AAS, BM), Camp Point, (between Square Bay and Calmette Bay), [67°58'S: 67°19'W], 27 October 1949, *B. Stonehouse* F.I.D.S. E627a (BM), Debenham Is. [68°08'S: 67°07'W], 39 m, 7 December 1947, *B. Stonehouse* F.I.D.S. E1116 (BM), Neny Fjord, Red Rock Ridge [68°18′S: 67°05′W], 120 m, 19 January 1948, *A. R. C. Butson* F.I.D.S. E1158 p.p. (BM), *c.* 12 m, 19 January 1948, *B. Stonehouse* F.I.D.S. E1176 (BM), Refuge I. [68°21′S: 67°10′W], 21–36 m, 29 November 1940, *H. M. Bryant* U.S.A.S. 32 (US); unlocalised, 'Terra Firma Land', 21 June 1936, *B.G.L.E.* 1482 (BM).

Uncertain determination

ARGENTINA. Tierra del Fuego: Sierra Alvear, S. slope, above Las Cotorras (*c.* 20 km ENE. of Ushuaia), 900–1000 m, 7 February 1940, *R. Santesson* 640e (640a p.p.) (S).

Race 2

CHILE. Aisén: Lago San Martin, Glaciares, *c.* 1500 m, 13 February 1933, *A. Donat* s.n. (H).

ARGENTINA. Río Negro: Parque Nacional Nahuel Huapí, Cerro Catedral, *c.* 2225 m, 6 January 1974, *A. Henssen & G. Vobis* 24677f (MB). Santa Cruz: Rio Fosiles, *c.* 1000 m, April 1905, *P. Dusén* s.n. p.p. (FI).

ANTARCTIC PENINSULA. Graham Land: Joinville I., N. end Active Sound [63°18′S: 57°56′W], 200 m, March 1981, *R. I. L. Smith* 3736 p.p. (AAS); Trinity Peninsula, Cape Longing [64°33′S: 58°50′W], 15–30 m, March 1961, *J. Killingbeck* 84 (AAS, BM, FH), 85 (AAS), 86 (AAS, FH), Duse Bay (as Race 1) *F.I.D.S.* D109-6 p.p. (BM), Crown Prince Gustav Channel, Egg I. [63°41′S: 57°42′W], 120 m, (as Race 1) F.I.D.S. D2756 (FH), Alectoria I. [63°59′S: 58°37′W], 30–60 m, 18 August 1945, *I. M. Lamb* F.I.D.S. D2467 (BM), foot of East Russell Glacier [63°44′S: 58°17′W], 14 December 1946, *A. Reece* F.I.D.S. D369–12a (FH), Vega I. [63°50′S: 57°25′W], False Island Point, 6–18 m, 5 December 1945, *I. M. Lamb* F.I.D.S. D2718 (BM), James Ross I. [63°55′S: 57′40°W], Herbert Sound, *c.* 90 m, 23 November 1945, *V. Russell* F.I.D.S. D2734 (BM), James Ross I., Cape Gage [64°12′S: 58°16′W], *c.* 6 m, 29 November 1945, *I. M. Lamb* F.I.D.S. D2843 (BM); Fallières Coast, Marguerite Bay, Neny Fjord, Roman Four Promontory [68°13′S: 66°58′W], 27 m, 8 December 1947, *B. Stonehouse* F.I.D.S. E1072a (BM); George VI Sound, Alexander I. [72°11′S: 69°05′W], Stephenson nunatak, *c.* 520 m, 5 December 1949, *V. E. Fuchs & R. J. Adie* F.I.D.S. E616-7 (BM), Alexander I., SE. corner, 385 m, 4 December 1949, *V. E. Fuchs* et al. F.I.D.S. E612 (BM).

Uncertain determination

ARGENTINA. Tierra del Fuego: Sierra Sorondo, N. slope above Las Cotorras (*c.* 20 km ENE. of Ushuaia), 800 m, 6 February 1940, *R. Santesson* 641c p.p. (S).

For details of specimens of uncertain determination (Race 2) from the Antarctic peninsula see specimens in AAS, BM and FH and list held in BM.

13. **Usnea subcapillaris** (D. Galloway) F. J. Walker, **comb. nov.** **Fig. 32**

Usnea ciliata var. *subcapillaris* D. Galloway in *N.Z. Jl Bot.* **6**: 470 (1968). – *Neuropogon subcapillaris* (D. Galloway) D. Galloway in *N.Z. Jl Bot.* **21**: 195 (1983). Type: New Zealand, South Island, Otago, Remarkables Range, 2000 m, on rock, February 1968, *D. J. Galloway* s.n. (CHR 343756 [OTA 68-222]! – holotype; CHR! – isotypes (2), BM! – isotype). [TLC: norstictic acid, salazinic acid, ± protocetraric acid, usnic acid.]

Description: Thallus (2)–5(–15) cm, arising from a ± delimited, pigmented holdfast, pendulous, rarely subdecumbent and spreading. Branching extensive, divergent, ± dichotomous, with numerous extended, delicate, capillaceous secondary branches predominating, and short attenuate, deflexed laterals; usually lacking fibrils. Branches terete, yellow-green, ± continuously pigmented or variegated violaceous black towards the apices. Cortex thin. Surface smooth, waxy, epapillate, easily fracturing, forming ± regular black-edged annulations. Medulla sublax towards the axis; axis occupying 0·3–0·5 of the branch diameter. Soredia, pseudoisidia and isidia absent. Apothecia rare, lateral, as in *U. ciliata*. Pycnidia not seen. TLC: (1) norstictic acid, salazinic acid, ± protocetraric acid, usnic acid; (2) squamatic acid, ± hypothamnolic acid, usnic acid; (3) psoromic acid, ± 2′-O-demethylpsoromic acid, usnic acid.

Distinguishing features: *Usnea subcapillaris* is characterised by its subdecumbent to pendulous habit, and a richly branched thallus with numerous, extended, fragile, divergent, flexuose-capillaceous secondary branches. It has a waxy, pigmented-annulate surface, a sublax medulla, containing depsides or depsidones, and occasionally apothecia of the '*ciliata*'-type.

Distribution: *Usnea subcapillaris* occurs mainly in the South Island of New Zealand; it is widely distributed in alpine localities, generally between 1000 and 2000 m, often alongside *U. ciliata*, although tending to favour slightly more sheltered aspects. This species is only known in

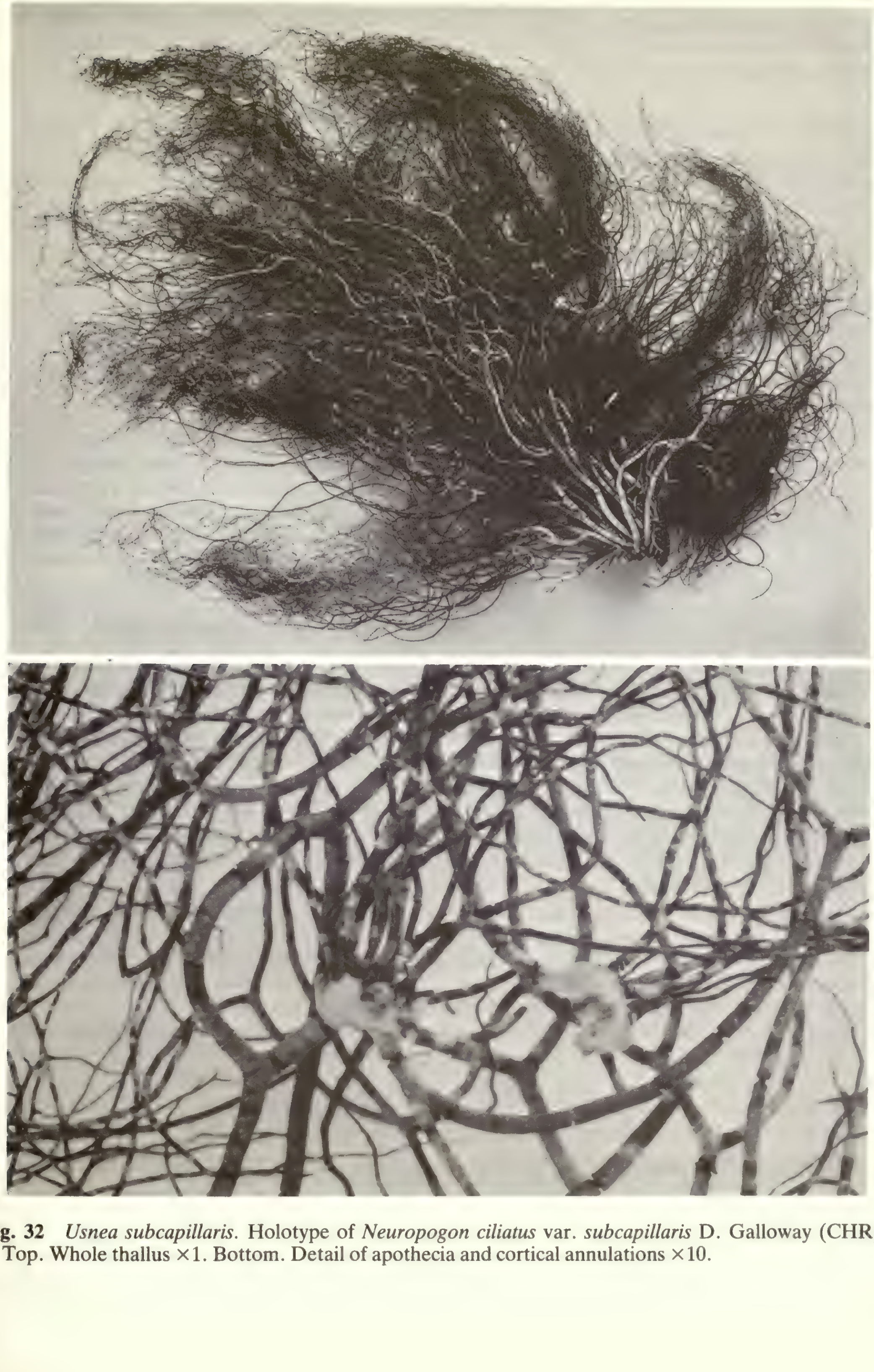


Fig. 32 *Usnea subcapillaris*. Holotype of *Neuropogon ciliatus* var. *subcapillaris* D. Galloway (CHR). Top. Whole thallus ×1. Bottom. Detail of apothecia and cortical annulations ×10.

the North Island from an unlocalised gathering (*Colenso* 2086, BM!, s.n., PC!) which was probably collected on the Ruahine Range. It is rare in Tasmania, being confined to a few high-altitude locations and the species was first identified from there by Bratt & Cashin (1976). Fig. 6.

Chemistry: Three chemical races have now been identified in *Usnea subcapillaris* (Galloway, 1984). Race 1 predominates whilst the other two races are very rarely encountered and are restricted to a few localities in mixed populations with Race 1. Protocetraric acid is only present in high concentrations in Race 1 and such thalli subsequently lack, or only contain traces of, norstictic and/or salazinic acids (for example, CHR 343473, herb. Bartlett 24724c). Interestingly, such chemical diversity does not occur in *U. ciliata* and *U. pseudocapillaris* or in the majority of Australasian populations of *U. acromelana*.

The presence of squamatic and hypothamnolic acids (Race 2) in the medulla of this species is unique within the subgenus and may easily be demonstrated by a brilliant white medullary fluorescence under UV light and a K+ purple reaction. Race 3, containing psoromic acid, is only known from a few localities, one of which, Mt. Hutt (CHR 343463, CHR 343483!), is unusual since some thalli have a mixed chemistry of two, or even all three, races.

Variation: The accounts of *Usnea ciliata* (p. 76), *U. acromelana* (p. 50), and *U. pseudocapillaris* (p. 90) may be referred to for much of the variation in branching, pigmentation, morphology, and anatomy found in *U. subcapillaris*. This species most closely resembles *U. ciliata* but differs in the pendulous habit, a more or less confined, rarely proliferating holdfast, repeated, divergent branching, and extensive, capillaceous, interwoven secondary branches. The medulla may also be slightly laxer, occupying a larger proportion of the branch diameter. The surface has more regularly spaced, conspicuous annulations which sometimes result in thallus fragmentation. When frequent on main branches, such annulations produce a characteristic segmented appearance, sometimes resulting in slight subsequent constrictions.

Secondary branches are more extensive than in *Usnea pseudocapillaris*, tending to form the most distinctive feature of the thallus, and are often up to two or three times the length of primary branches. The fragile and fragmentary nature of the secondary branches becomes more pronounced on storage. Adjacent thalli of richly branched specimens, with diverging ultimate branches, often become mutually entangled. *U. pseudocapillaris* and *U. subcapillaris* are only likely to be confused when they are immature and lack any reproductive structures.

In less typical forms the secondary branches are somewhat coarser, although thalli are still moderately to richly branched and retain the characteristic divergent habit with short, attenuate ultimate branches. This is a particular feature of some Tasmanian collections in which there is a gradual transition between the coarse primary branches and the capillaceous secondary branches which are shorter, broader and more frequently divided than in the majority of New Zealand specimens examined.

Apothecia are rare in New Zealand whilst in Tasmania they are only known from a single collection (HO 35239!). They are usually lateral on secondary branches and have a subtending, extended apical branch or spur which frequently divides. They are usually smaller, *c.* 5 mm, than in *Usnea ciliata* and pigmentation of the disc may rarely be undeveloped. Marginal excipular rays vary in number but are usually longer, finer and may divide, thus resembling secondary branches. Their scarcity may be a reflection of the ease at which the thallus fragments and regenerates, thus providing an alternative method of reproduction. This might explain the wider distribution of this species than *U. ciliata* in Australasia.

Species concept: *Usnea subcapillaris* is now considered (Galloway, 1983) to be a distinct species from *U. ciliata* and a parallel can now be found between the related species, *U. pseudocapillaris* and *U. acromelana*. *U. subcapillaris* may also be regarded as the fertile counterpart to *U. pseudocapillaris* within the *U. ciliata* complex. It may be distinguished from *U. ciliata* by the pendulous or subdecumbent habit resulting from repeated, more or less divergent, dichotomous, division of extensive, capillaceous, secondary branches which give a fragile, lax, combed or frequently entangled appearance. Other characteristic features include the shorter, often widely divaricately branched main branches and sometimes the slightly laxer nature of the medulla and deep fissured annulations. It is extremely rare for thalli to be encountered that are difficult to assign to *U. subcapillaris* or *U. ciliata*. Coarser, suberect, or subdecumbent forms from Tasmania are included within the accepted variation.

There does not appear to be any correlation between chemical race and morphological variation.

Usnea subcapillaris may be distinguished from the other fertile species of *Neuropogon* by its restricted distribution besides morphological characters.

Selected specimens examined

Race 1

AUSTRALIA. Tasmania: Mt. Wellington, summit, 1250 m, 15 March 1970, *G. Degelius* A-414 (herb. Degelius), 1250 m, 20 December 1964, *G. C. Bratt* 1872a (CHR 343280), 'Table Mountain' [Mt. Wellington], (part of type gathering of *U. acromelana* var. *decipiens* Lamb (BM)); Central Plateau, Mt. Penny, near Arthur's Lake, 1134 m, 4 April 1969, *G. C. Bratt & K. M. Mackay* 69/161 (CHR 343323, HO 35239 p.p.); Table Mountain, 1095 m, 18 June 1972, *G. C. Bratt & J. A. Cashin* Bratt 72/393 p.p. (HO 35178), Bratt 394 (HO 35179); Sandbank Tier, 5 April 1969, *G. C. Bratt* 69/212 (HO 35195); Seager's Lookout, *c.* 10 km NNW. of Maydena, 1240 m, 30 May 1970, *G. C. Bratt & F. N. Larkin* Bratt 70/680b p.p. (HO 35236 p.p.).

NEW ZEALAND. North Island. unlocalised [Ruahine Range?], *Colenso* 2086 (BM), s.n. (PC).

South Island. Nelson: saddle between Mt. Aorere and Mt. Cobb, *c.* 1580 m, 19 December 1982, *J. K. Bartlett* 247246 p.p. (BM); Mt. Robert, Lake Rotoiti, 1430 m, 16 January 1960, *D. Scott* s.n. (BM, OTA); St. Arnaud Range, Lake Rotoiti, 1520 m, February 1959, *Mason* 647 (BM, OTA), St. Arnaud Range, 1680 m, 22 December 1967, *A. F. Mark* s.n. (CHR 343290 p.p., CHR 343476); Mt. Technical, above Lewis Pass, 14 January 1979, *D. J. Galloway* s.n. (CHR 343275); Lake Sylvester, 1620 m, 18 December 1967, *A. F. Mark* s.n. (CHR 343488); Lake Peel, 1430 m, *J. K. Bartlett* s.n. (CHR 343223). Marlborough: Black Birch Range, nr. Altimarlock trig, 10 January 1971, *L. B. Moore* s.n. (CHR 162621); Inland Kaikoura Range, Mt. Mitre, 2 January 1954, *R. Mason & D. R. McQueen* 2760 (CHR 160686). Canterbury: Mackenzie Country, Lower Godley River Valley, 1830 m, 21 December 1958, *D. Scott* 99 (BM, OTA); Torlesse Range, Foggy Peak, summit rocks, 1680 m, 18 December 1962, *P. W. James* 1918 (BM), 1680 m, November 1972, *D. J. Galloway* s.n. (CHR 343491), 12 November 1972, *G. C. Bratt* 72/1880b (HO 35170); Kirkliston Range, 1680–1830 m, 25 March 1978, *D. J. Galloway* s.n. (CHR 343178, CHR 343252 p.p.), 1830 m, December 1964, *C. J. Burrows* s.n. (CHR 343477); Mt. Peel, 1740 m, January 1972, *D. J. Galloway* s.n. (CHR 343437 p.p., CHR 343499); Mt. Cook National Park, Mt. Annan, 2740 m, *R. B. Filson* s.n. (MEL 1026826); Arthur's Pass, Mt. Bealey, 1680 m, 19 August 1968, *L. D. Kennedy* s.n. (CHR 343452); Two Thumb Range, Mt. Richmond, November 1968, *A. F. Mark* s.n. (CHR 343489 p.p.). Otago: Rock and Pillar Range, 1160–1190 m, 18 September 1981, *F. J. Walker* s.n. (BM), S. end, 980 m, June 1967, *T. S. Choate* s.n. (CHR 343347), 1480 m, February 1967, *D. J. Galloway* s.n. (CHR 343490), 980 m, June 1967, *D. J. Galloway* s.n. (CHR 342766); Young Range, 1430 m, March 1968, *D. J. Galloway* s.n. (CHR 343447 p.p., CHR 343472); Old Man Range, 1490 m, November 1962, *P. W. James* 443b (BM), 1130 m, 1 February 1963, *P. W. James* 1579 (BM), 1220 m, 1 February 1963, *P. W. James* 1597 (BM), 1680 m, April 1968, *D. J. Galloway* s.n. (CHR 343467, CHR 343478, CHR 343497), 1968, *D. J. Galloway* s.n. (CHR 343492), 1490 m, 30 August 1968, *L. D. Kennedy* s.n. (CHR 343479), 1520 m, *A. F. Mark* s.n. (CHR 343470); Mt. Pisa, 1920 m, March 1968, *D. J. Galloway* s.n. (CHR 343468, CHR 343475, CHR 343480, CHR 343494), 1860 m, March 1968, *D. J. Galloway* s.n. (CHR 343473, CHR 343486), March 1968, *D. J. Galloway* s.n. (CHR 343448); Rees Valley Slopes, Leary Peak, 1680 m, January 1968, *D. J. Galloway* s.n. (CHR 343474, CHR 343287); Coronet Peak, 1520 m, February 1968, *D. J. Galloway* s.n. (CHR 343471); Humboldt Mtns, Mt. Minos, 2010 m, 1 January 1970, *D. J. Galloway* s.n. (CHR 343338, CHR 343488, CHR 343499); Mt. Erebus, 1980 m, 14 January 1970, *D. J. Galloway* s.n. (CHR 343754); Bedford Valley, 1680 m, 26 December 1970, *D. J. Galloway* s.n. (CHR 343482); Remarkables, 1980 m, March 1966, *D. J. Galloway* s.n. (CHR 343487); Coronet Peak, 1520 m, February 1968, *D. J. Galloway* s.n. (CHR 343755); Shepherd's Pass, 1980 m, January 1968, *D. J. Galloway* s.n. (CHR 343450); Mt. Brewster, 2130 m, March 1968, *D. J. Galloway* s.n. (CHR 343493); Mt. Roy, 1 November 1972, *G. C. Bratt* 72/1506 (HO 35175); Unnamed Virgin, N. of Pope's Nose, 2350 m, 11 February 1969, *L. D. Kennedy* s.n. (CHR 342787 p.p.); Mt. Pisgah, *c.* 1600 m, *J. S. Thomson* 1983 (CHR 343797).

Race 2

NEW ZEALAND. South Island, Nelson: above Cobb Lake, 1070 m, December 1967, *A. F. Mark* s.n. (CHR 343498). Canterbury: Four Peaks Range, Blue Mountain, *c.* 1640 m, 23 April 1979, *D. J. Galloway* s.n. (CHR 343228), 23 April 1979, *D. J. Galloway* s.n. (CHR 343179); Mt. Peel, 1740 m, January 1972, *D.*

J. Galloway s.n. (CHR 343500); Mt. Hutt, 1520 m, *C. J. Burrows* s.n. (CHR 343495 p.p.), 1830 m, *C. J. Burrows* s.n. (CHR 343483 p.p.); Two Thumb Range, Mt. Richmond, November 1968, *A. F. Mark* s.n. (CHR 343489 p.p.). Otago: Sugarloaf Saddle, 1070 m, May 1966, *D. J. Galloway* s.n. (CHR 343446 p.p.), 1280 m, February 1968, *D. J. Galloway* s.n. (CHR 343408 p.p.); Young Range [as Race 1] (CHR 343477 p.p.), 1520 m, March 1968, *R. Nilsson* s.n. (CHR 343481); Humboldt Mtns, Mt. Nox, 1950 m, 31 December 1969, *D. J. Galloway* s.n. (CHR 342791, CHR 343469).

Race 3

NEW ZEALAND. South Island, Canterbury: Mt. Hutt, *C. J. Burrows* s.n. [as Race 2] (CHR 343463 p.p., CHR 343483 p.p.); Four Peaks Range, Tripps Peak, 24 April 1979, *D. J. Galloway* s.n. (CHR 343337 p.p.). Otago: Rock and Pillar Range, 1280 m, December 1964, *D. J. Galloway* s.n. (CHR 343286, CHR 343451), 1400 m, July 1968, *L. D. Kennedy* s.n. (CHR 343496), 1400 m, February 1967, *D. J. Galloway* s.n. (BM).

For further localities see Galloway (1968) and lists held in BM.

14. **Usnea taylorii** J. D. Hook. **Figs 33–34**

in Hooker & Taylor in *Lond. J. Bot.* **3**: 657 (1844). – *Alectoria taylorii* (J. D. Hook.) Nyl. in *Mém. Soc. Imp. Sci. Nat. Cherbourg* **5**: 98 (1857). – *Neuropogon taylorii* (J. D. Hook.) Nyl., *Synops. Lich.* **1**: 273 (1860). Type: Kerguelen's Land, Antarctic Expedition of H.M.S. Discovery ships 'Erebus' and 'Terror' 1839–1843, *J. D. Hooker* (BM! – lectotype, selected here; BM!, E!, FH, not seen, M! – isolectotypes). [TLC: no medullary substances, usnic acid.]

Note: The epithet *'taylori'* is corrected to *'taylorii'* under Article 73.10 following Recommendation 73C.1. Many original collections were widely distributed by Hooker and the species is best lectotypified on the collection illustrated by Lamb (1939*a*) in BM in preference to the herb. Taylor collection (FH) indicated by Dodge (1948).

Description: Thallus (4)–5–7(–10) cm, arising from a proliferating, rarely pigmented, holdfast, erect, monopodial to ± dichotomous, infrequently branched above with ± flexuose, tapering to subcornute apices. Branches terete, corneous, yellow-green, continuously or irregularly pigmented with black pigment towards the apices. Cortex thin. Surface ± subnitid, epapillate, ± smooth but mottled with slightly raised, unpigmented maculae. Medulla compact, reduced, invading axial cavities. Axis occupying *c.* 0·9 of the branch diameter, partially sub-divided, forming several strands, frequently abutting the cortex and protruding to form pale maculae. Soredia, pseudoisidia and isidia absent. Apothecia frequent, subterminal with a prominent, geniculate spur or rarely lateral and subsessile; ± cupular, plane or sinuose-deflexed on maturity. Disc black, excipulum smooth or minutely faveolate, margin ± excluded, rays absent. Pycnidia rare towards apices. TLC: (1) fumarprotocetraric acid (trace), usnic acid; (2) no medullary substances, usnic acid.

Distinguishing features: *Usnea taylorii* is characterised by its erect, proliferating habit and a monopodial to infrequently branched, often extensively pigmented, corneous thallus; a subnitid maculate surface, a much reduced medulla, usually lacking medullary substances, a broad, sub-divided axis and subterminal, geniculate apothecia with a black disc lacking excipular rays.

Distribution: *Usnea taylorii* is endemic to Kerguelia. Material has been examined from Îles Kerguelen and Îles Crozet and Dodge & Rudolph (1955) have recorded the species from Heard Island (*A.N.A.R.E.* 250, MEL, not seen). Specimens from South America misidentified as *U. taylorii* by Räsänen (H!) are referable to *U. perpusilla*. Specimens collected by Hooker, apparently from South America, are erroneously labelled (see p. 69). *U. taylorii* replaces *U. aurantiaco-atra* in Kerguelia and is often found in communities there with *U. antarctica* and *U. trachycarpa*. Fig. 4.

Chemistry: All collections examined from Îles Kerguelen lack medullary substances, including fatty acids. Race 1, containing low concentrations of fumarprotocetraric acid, is only recorded from the single collection from Îles Crozet.

Variation: This is probably the most distinctive species of the subgenus. It has a unique axis structure throughout the thallus giving rise to the formation of separate axial strands that are

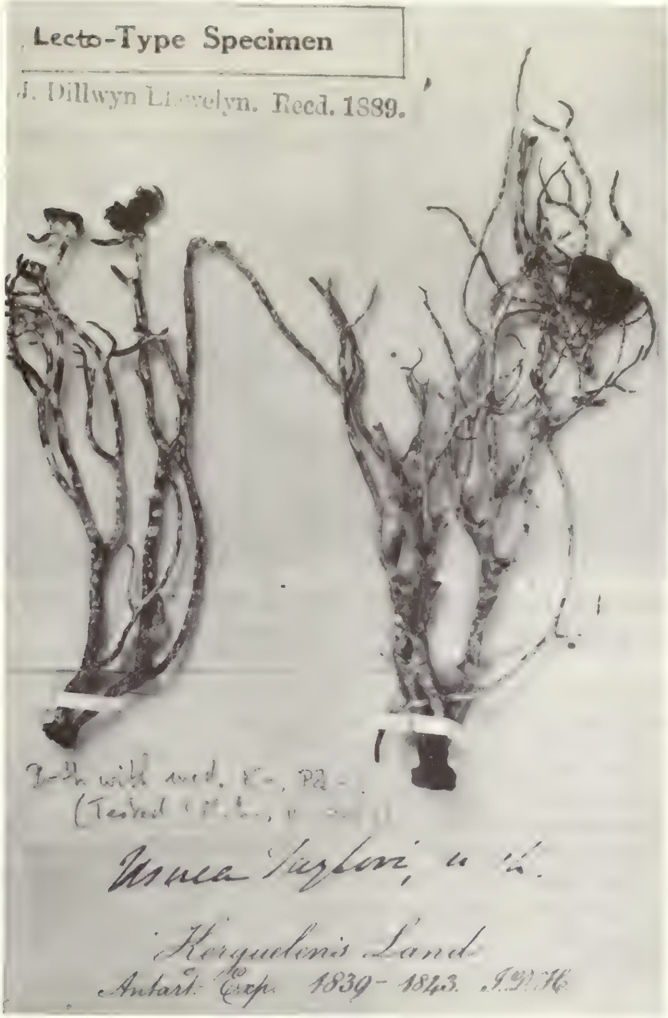

Lecto-Type Specimen
J. Dillwyn Llewelyn. Recd. 1889.
Usnea Taylori, n. sp.
Kerguelen's Land
Antart. Exp. 1839–1843. J.D.H.

Fig. 33 Lectotype of *Usnea taylorii* J. D. Hook. (BM) ×1.

invaded by medullary tissue, resembling a coaxial cable; as illustrated by Rienke (1895). The extrusion of the axis through the narrow medulla and the otherwise cortex produces the characteristic pale, raised maculae that resemble the pseudocyphellae of *Alectoria ochroleuca* on an otherwise smooth surface. This often results in a mottled, rather than variegated, pattern on the extensively pigmented ultimate branches. Very rarely these maculae may form papilla-like structures which remain ecorticate.

Collections are mostly uniform, the only variation being in the extent of thallus branching and pigmentation which range from scantily pigmented unbranched thalli to more richly branched forms that are extensively pigmented towards the apices. Main branches are usually thick and corneous, and are often flexuose with tapering, subcornute apices, giving the thallus a sinuose habit.

Apothecia are characteristically subterminal and are particularly conspicuous on sparingly branched thalli. In contrast, in more richly branched thalli apothecia tend to be smaller, slightly cupular, subsessile, and lateral. Pycnidia are rare, and may be confused with a range of

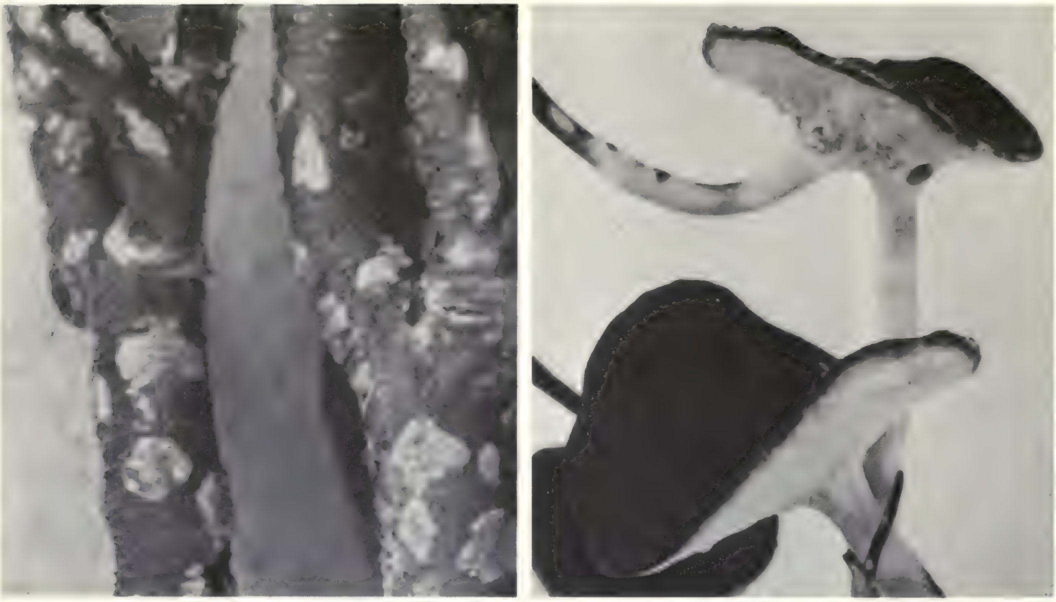


Fig. 34 *Usnea taylorii.* Left. Detail of maculae. Challenger Exped. 1874, *Molseley* (BM) ×10. Right. Detail of apothecia. Îs. Kerguelen, January 1960, *Tilman* (BM) ×10.

parasites, including *Lecidea alectoriae* which was originally described (W. Lindsay, 1859) from this species.

Species concept: *Usnea taylorii* appears to be a highly evolved species which may be closely related to *U. aurantiaco-atra. U. taylorii* replaces *U. aurantiaco-atra* in the Kerguelen region and shares several morphological characteristics besides the existence of a race containing fumarprotocetraric acid. *U. aurantiaco-atra* does not occur east of Bouvetøy where populations lack depsidones, have a very thick axis, and a reduction in the extent of papillation. A sorediate counterpart is not known, although some populations of *Usnea antarctica*, previously described as distinct taxa, for example *U. crombiei* (Dodge, 1948) and *U. insularis* (Lamb, 1939*a*), have slightly irregular but undivided axes.

Usnea taylorii may be distinguished from all other fertile species within the subgenus by the unique branch anatomy with the production of maculae.

Specimens examined
Race 1
Îs. CROZET. (unlocalised) *c.* 610 m, 1959–60, *W. H. Tilman* s.n. (BM).
Race 2
Îs. KERGUELEN. Cliffs above Lake du Val Studer, 11 February 1963, *R. B. Filson* 4665 p.p. (BM); Swain's Bay and Observatory Bay, Venus Transit Exped. 1874–75, *A. E. Eaton* s.n. (BM, E, M), *A. Balfour* s.n. (E); Royal Sound, *A. E. Eaton* s.n. (UPS), Royal Sound, nr. Port Jeanne d'Arc, *c.* 460 m, 11 February 1930, *B.A.N.Z.A.R.E.* B176 (AD, FH); Crater Hill, Christmas Harbour and Cumberland Bay, Ross' Antarctic Exped. 1839–43, *R. McCormick* s.n. (BM); Baie des Baleiniers, Petit Mt. Ballon, 300 m, January 1960, *W. H. Tilman* s.n. (BM, FH); unlocalised – Challenger Exped., January 1874, *H. N. Moseley* s.n. (BM); Challenger Exped. (GLAM NHB 1927-8-348, GLAM NHB 1927-8-349); *O. Ring* s.n. (O); March 1931, *A. de la Rue* s.n. (UPS); December 1898, *W. Schimper* s.n. (UPS).
HEARD I. see Dodge & Rudolph (1955).

15. **Usnea trachycarpa** (Stirton) Müll. Arg. **Fig. 35**

in *Nuovo G. bot. ital.* **21**: 37 (1889). – *Neuropogon trachycarpus* Stirton in *Scott. Nat.* **6**: 105 (1881). Type: Kerguelen's Land (So. Antarctic), [January, 1875], *Challenger Exped.* 6 (BM! – holotype; BM! – isotype). [TLC: norstictic acid, fatty acids, usnic acid.] (see Note)

Usnea naumannii Müll. Arg. in *Bot. Jb.* **4**: 54 (1883). Type: Kerguelen, Betsys Cove, 1875, *Dr Naumann* (G! – holotype). [TLC: norstictic acid, ± fatty acids, usnic acid.]

Usnea melaxantha var. *angulosa* Müll. Arg. in *Flora, Jena* **71**: 528 (1888). – *Usnea sulphurea* var. *angulosa* (Mull. Arg.) Zahlbr., *Cat. Lich. Univers.* **6**: 603 (1930). Type: Argentina, Patagonia [unlocalised], *Claraz* (G! – holotype). [TLC: ± norstictic acid, usnic acid.]

Usnea trachycarpa var. *sublaevis* Müll. Arg. in *Hedwigia* **34**: 139 (1895). Type: *Lich. Exot.* 141, [Argentina] Patagonia, Moreno, 1894, *Otto Kuntze* 713 (G! – holotype). [TLC: no medullary substances, usnic acid.]

Usnea trachycarpa var. *trachycarpoides* Vainio, *Rés. Voy. S. Y. Belgica, 1897–99, Botan., Lichens:* 12 (1903). – *Neuropogon trachycarpus* f. *trachycarpoides* (Vainio) Lamb in *J. Linn. Soc.* (Bot.) **52**: 233 (1939). – *Usnea trachycarpoides* (Vainio) Dodge, *Lich. Fl. Antarct. Cont.:* 238 (1973). Type: Argentine, Île des Etats, Golfe Saint Jean, lat. 55°24′S, sur les parois verticales, 1898 *M. Émile G. Racovitza* 182 (TUR! – holotype). [TLC: norstictic acid, salazinic acid, ± protocetraric acid, usnic acid.]

Usnea hyyppae Räsänen in *Suomal. eläin-ja kasvit. Seur. van. kasvit. Julk.* **2**(1): 11 (1932). Type: [Argentina] Fuegia media, Cerro Milladeo, reg. alp. 800 m.s.m., Expeditio Fennica 1928–29, *H. Roivainen* (H! – holotype; H! – isotype). [TLC: no medullary substances, usnic acid.]

Usnea taylorii var. *subciliata* Räsänen in *Suomal. eläin-ja kasvit. Seur. van. kasvit. Julk.* **2**(1): 11 (1932). Type: [Chile] Fugia media, Cerro Chico, reg. alp. 550 m.s.m., Expeditio Fennica 1928–29, *H. Roivainen* (H! – holotype). [TLC: no medullary substances, usnic acid.]

Neuropogon substrigulosus Lamb in *J. Linn. Soc.* (Bot.) **52**: 231 (1939). – *Neuropogon trachycarpus* f. *substrigulosus* (Lamb) Lamb in *Lilloa* **14**: 156 (1948). – *Usnea substrigulosa* (Lamb) Dodge. *Lich. Fl. Antarct. Cont:* 237 (1973). Type: Falkland Islands, (no collector given) (BM! – holotype). [TLC: norstictic acid, salazinic acid, ± protocetraric acid, fatty acids, usnic acid.]

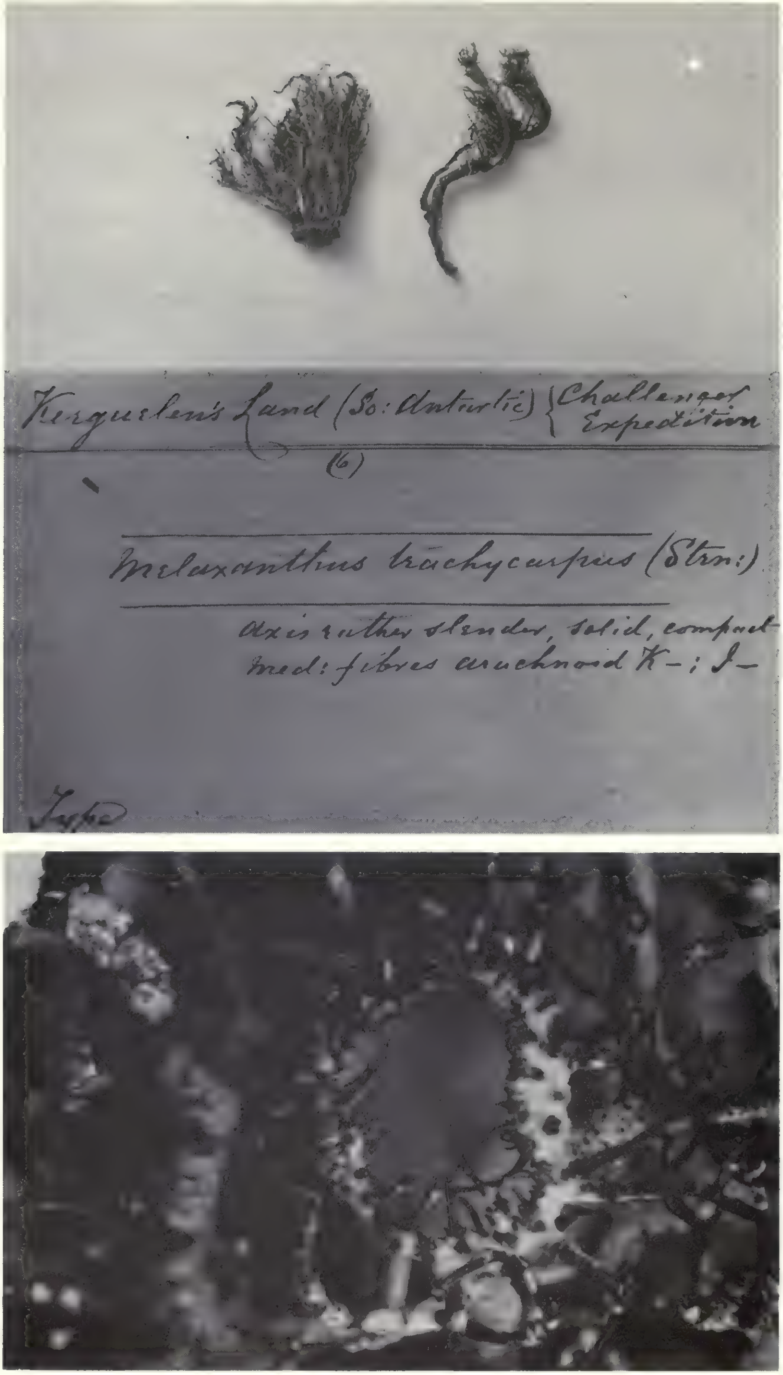
Neuropogon trachycarpus f. *elatior* Lamb in *Lilloa* **14**: 157 (1948). Type: [Argentina] Tierra del Fuego, Sierra Alvear, the Southern slope, above Las Cotorras (*c.* 20 km ENE. of Ushuaia), rocks in the alpine region, 900–1000 m, 1940, *R. Santesson* 640b, (S! – holotype; S!, CANL 17258! – isotypes). [TLC: no medullary substances, usnic acid.]

Note: The specimens figured by Lamb (1939*a*) are only part of the holotype material of *Neuropogon trachycarpus* and were selected from Stirton's herbarium by Miss A. L. Smith and are here regarded as an isotype. The original capsule bearing Stirton's handwriting was mislaid and not traced by Lamb or Dodge (1948). This capsule has recently been traced in the BM and bears the inscription 'Kerguelen's Land (So. Antarctic) Challenger Expedition (6) – melaxanthus trachycarpus (Strn.) axis rather solid, compact. Med. fibres arachnoid. K–; I–. Type.' This material forms the holotype and consists of two slightly larger thalli than the isotype, one of which bears three small apothecia.

Description: Thallus (2–3)–4(–7–9) cm, arising from a proliferating, unpigmented, holdfast, erect, monopodial or ± dichotomous, infrequently to moderately branched above. Fibrils numerous on all branches, short, *c.* 5 mm, spreading, ± variegated or continuously black-pigmented. Branches terete or rarely slightly angular, yellow-green, ± continuously pigmented towards the apices. Cortex variable in thickness. Surface matt, ± smooth at the base becoming markedly faveolate to richly papillate or scabrid with numerous conspicuous fibrils above. Medulla lax or sublax, axis occupying 0·3–0·5 of the branch diameter. Soredia, pseudoisidia and isidia absent. Apothecia frequent, subterminal, ± cupular, expanding on maturity. Disc rufous brown, excipulum faveolate to verrucose-papillate with numerous marginal, attenuate, ± pigmented rays. Pycnidia infrequent towards apices. TLC: (1) norstictic acid, ± salazinic acid, ± protocetraric acid, ± 2–6 fatty acids (murolic acid complex), usnic acid; (2) psoromic acid, 2′-O-demethylpsoromic acid, ± 2–6 fatty acids (murolic acid complex), usnic acid; (3) no medullary substances, ± 2–6 fatty acids (murolic acid complex), usnic acid.

Distinguishing features: *Usnea trachycarpa* is characterised by its erect, proliferating habit, an infrequently branched thallus with numerous fibrils, a faveolate-papillate surface, a lax to sublax, arachnoid, medulla, often containing depsidones and fatty acids, a thin axis, and subterminal apothecia with a rufous brown disc with numerous marginal and submarginal excipular rays.

Distribution: *Usnea trachycarpa* is known from southern South America (Patagonia and Tierra del Fuego) as far north as latitude *c.* 42°S, the Falkland Islands and Îles Kerguelen, and has also been recorded by Dodge & Rudolph (1955) from Heard Island (*Gilchrist* 2, MEL,



Kerguelen's Land (So: Antarctic) {Challenger Expedition

(6)

Melaxanthus trachycarpus (Strn:)

Axis rather slender, solid, compact
med: fibres arachnoid K- ; I-

Type

Fig. 35 *Usnea trachycarpa*. Top. Holotype of *Neuropogon trachycarpus* Stirton (BM) ×1. Bottom. Detail of apothecium. Patagonia, *James* 28 (BM) ×10.

not seen). A single, sterile specimen from the Antarctic peninsula is tentatively referred to this species (*R. I. L. Smith* 3453 p.p., AAS!), although it is not known elsewhere in Antarctica or the islands of the Scotia Arc. A thallus fragment amongst the type of *U. acromelana* var. *decipiens* (BM!) from Tasmania appears to belong to this species, but is probably misplaced since the species is not otherwise known in Australasia.

Usnea trachycarpa is a characteristic species of dry, exposed conditions and is frequently found at relatively low altitudes, for example near sea-level to *c.* 200 m on Îles Kerguelen and the Falkland Islands. It has a broader altitudinal range in South America, ranging from 30 to 1000 m in Tierra del Fuego and Santa Cruz up to *c.* 2250 m further north in Río Negro.

In the Falkland Islands this species is often replaced by *Usnea aurantiaco-atra* whilst in southern South America it is sometimes found in communities with *U. aurantiaco-atra* and *U. perpusilla* and a range of asexual species, particularly *U. patagonica*. Fig. 5.

Chemistry: The most common race throughout the range of *Usnea trachycarpa* is Race 1, containing norstictic acid, usually with salazinic acid, and frequently with detectable (by TLC) concentrations of connorstictic acid and/or protocetraric acid. An additional unknown substance that was yellow after charring (Rf class TDA 1, HEF 2-3) was found in some thalli from Îles Kerguelen, but did not appear to be of taxonomic significance.

Race 2, containing psoromic acid, is very rare and is only known from a few collections from a single locality in Argentina.

Up to six fatty acids of the murolic acid complex (see p. 14) occur in *Usnea trachycarpa* and have been demonstrated by TLC in all three chemical races, although their presence and number may vary within a single collection. They are particularly persistant in Race 1 from Îles Kerguelen, whilst from elsewhere their distribution appears to be more spasmodic, for instance only occurring in about half a selection of 30 South American specimens tested. The UV+ unknowns were only rarely detected in this species.

Variation: *Usnea trachycarpa* is, especially when fertile, an easily recognised and uniform species throughout its range. The extent of branching is reminiscent of *U. ciliata* (p. 76). Thalli range from virtually monopodial forms, often scantily pigmented at the apices of branches and fibrils, to more richly branched, extensively pigmented forms that are characteristic of higher altitudes and more exposed localities. Papillae are only pigmented in the more extensively pigmented, high-altitude forms. Some populations are more robust, up to *c.* 9 cm tall, and have previously been recognised as distinct taxa, for example *Neuropogon substrigulosus* and *N. trachycarpus* f. *elatior*.

The number and extent of fibrils is variable although they are nearly always present; forming a characteristic feature of the species. The surface is smooth, matt and free from fibrils near the holdfast, but becomes papillate-faveolate above with the production of small, uniform fibrils of *c.* 5 mm in length. Only very rarely is the thallus smooth to minutely papillate throughout, with fewer fibrils. Various taxa have been described based on the extent of fibril production and range from specimens virtually free of fibrils, including *Usnea trachycarpa* var. *sublaevis* and *U. taylorii* var. *subciliata* from Argentina, to extensively fibrillar forms, including *Neuropogon substrigulosus* from the Falkland Islands.

The type specimen from Îles Kerguelen, although small, is fairly typical of the species. However, the medulla is more compact than is frequently found in more robust specimens, as seen in the type of *Usnea naumannii* from the same island group, although it still possesses an arachnoid texture, and slight inflation and characteristic faveolation of main branches. The degree of laxness and hence relative widths of medulla and axis, are the most variable feature of this species. Many gatherings from Patagonia are typical of a laxer form, for example the types of *U. melaxantha* var. *angulosa* and *U. hyyppae*, whilst in *Neuropogon trachycarpus* f. *elatior* the medulla is extensive and lax with the axis only occupying about a third of the branch diameter.

Apothecia are uniform and are normally subterminal. When young they are cupular but are partially expanded on maturity, sometimes becoming irregular. The disc is always rufous brown in freshly collected specimens and quite distinct from the colour of the thallus. The disc only rarely becomes partly blackened when moribund. The extent and length of excipular rays may vary. These are usually fine, short, unbranched, black-pigmented or variegated, and are numerous around the margin or the excipulum and less frequent over the rest of the surface. Variation in number, thickness and length of rays has led to the description of distinct taxa, including *Usnea taylorii* var. *subciliata* and *Neuropogon substrigulosus*.

Species concept: Variation in thallus size, ornamentation, morphology, pigmentation, and anatomy in *Usnea trachycarpa* is not considered sufficient to recognise additional or infraspecific taxa; a parallel can be drawn within *U. aurantiaco-atra*. Reduction in the extent of black pigmentation, including the presence of a rufous brown pigment in the apothecial disc, may indicate some affinities with species of *Usnea* subgenus *Usnea* (see p. 43), for example *U. hieronymii* (var. *adusta*) and *U. densirostra*, which are saxicolous, have fibrils, a pale buff disc, and exhibit very limited pigmentation. These species have a more northern distribution and are not characteristic of montane areas.

Usnea trachycarpa is possibly the primary species of *U. subantarctica* and may also be closely related to *U. patagonica* and *U. neuropogonoides* (see p. 42). It may easily be distinguished from all other fertile species of the subgenus by the rufous brown apothecial disc with numerous short rays and, even when sterile, by the numerous fibrils on all branches.

Selected specimens examined
Race 1
CHILE. Magallanes: Magellan Straits, Punta Arenas, *Steinmann* s.n. (BM, H, M, PC); Natales, Cerro Dorotea, 9 May 1940, *R. Santesson* 2135 (S), *R. Santesson* 2136 (S); Tierra del Fuego, Isla Navarino, Puerto Navarino, 10 m, 28 February 1940, *R. Santesson* 1232a (UPS, S); Cabo de Hornos, Cape Spencer, *J. D. Hooker* s.n. (BM).
ARGENTINA. Santa Cruz: Lago Argentino, Cerro del Fraile, near Estancia Lago Roca, 270 m, 1958–59, *P. W. James* 764 (BM); Lago Argentino, Cordillera Cristales, Cerro del Fraile, *c.* 1000 m, 26 December 1958, *P. W. James* 29 (BM); hills above Calafate, 1235 m, 1958–59, *P. W. James* 420a (BM); Calafate, 'weg nach' Punta Bandera, Campo Anita Fuss des Co. Moyano, *c.* 500 m, December 1973, *A. Henssen & G. Vobis* 24540b (MB); Lago Viedma, 1200 m, 2 April 1903, *P. Dusén* s.n. (H); Rio Fósiles, *c.* 1000 m, 1975. *P. Dusén* s.n. (FH, H, M p.p., WU 2997 p.p.); Depto. Guar Aiken, 60 km SW. of Rio Gallegos, 30 m, 4 January 1939, *W. J. Eyerdam* et al. 24093 (BM p.p., FH). Tierra del Fuego: Parque Nacional Tierra del Fuego, Ushuaia, 'weg zum' Glacier Martial, *c.* 750 m, 7 December 1973, *A. Henssen & G. Vobis* 24420j (MB); Ushuaia, small island in Beagle Channel, 30 January 1940, *R. Santesson* 525 p.p. (S); Sierra Alvear, S. slope, above Las Cotorras, *c.* 20 km ENE. of Ushuaia, 650 m, 9 February 1940, *R. Santesson* 636b (S, UPS).
FALKLAND IS. East Falkland Is.: Goose Green, Fish Creek, 9 m, 22 September 1963, *R. W. M. Corner* 67 (AAS); Mt. Longdon, near Port Stanley, 174 m, 2 April 1967, *D. C. Lindsay* 1657 (AAS), *D. C. Lindsay* 1660 (AAS), *D. C. Lindsay* 1661 (AAS); Fairy Cove, near Port Stanley, near sea-level, 30 January 1946, *I. M. Lamb* F.I.D.S. 2892 (BM, CANL 17257); N. of Wireless Hill, 100 m, 28 February 1977, *R. I. L. Smith* 2571 (AAS); Port Stanley, *W. Lechler, pl. ins. Maclovian.* 69c (BM, M); Murray Heights and Lookout Rocks, Stanley, 30 March 1965, *J. Price* s.n. (BM). West Falkland Is.: Crooked Inlet, Roy Cove, 31 August 910 (collector unknown) (BM); Cooke Hill and Roy Cove, 1909–11, *E. Vallentin* 89 (BM).
Îs. KERGUELEN. Royal Sound, Venus Transit Exped. 1874–75, *A. E. Eaton* s.n. (BM, E, M, UPS); Swain's Bay, Venus Transit Exped. 1874–75, *A. E. Eaton* s.n. (BM, E, M); Observatory Bay, Venus Transit Exped. 1874–75, *A. E. Eaton* s.n. (BM, E, M); Molloy Point, Venus Transit Exped. 1874–75, *J. P. Kidder* s.n. (FH); Baie Islandaise (Baie des Baleiniers), 210 m, January 1960, *W. H. Tilman* s.n. (BM, FH); above Lake du Val Studer, 11 February 1963, *R. Filson* 4665 p.p. (BM).
Race 2
ARGENTINA. Santa Cruz: Depto. Guar Aiken [as Race 1], *W. S. Eyerdam* et al. 24093 (BM), Guar Aiken, 18 January 1940, *R. Santesson* 300a (S, UPS), *R. Santesson* 300b (S).
Race 3
CHILE. Aisén: Coyhaique Alto, 1000 m, 18 November 1940, *R. Santesson* 4600 (S), *R. Santesson* 4632 p.p. (S), *Lich. Austro-amer. ex Herb. Regnelliano* 423 (BM, M, UPS, S).

ARGENTINA. Neuquén: Paso do Pino Hachado, 13 November 1941, *Pérez Moreau* 5982 (H). Río Negro: Parque Nacional Nahuel Huapí, Cerro Catedral, *c.* 2225 m, 6 January 1974, *A. Henssen & G. Vobis* 24677e (MB); Cerro Leones, 1 January 1974, *A. Henssen & G. Vobis* 24625 p.p. (MB). Chubut: Rio Corcovado, February 1903, *Illin* 553 (BM); Pampa Chica, 13 November 1908, *C. Skottsberg* s.n. (UPS). Santa Cruz; Patagonia, Lago Argentino, *C. Megluno* s.n. (BM); Rio Gallegos, Estancia Stag River, *R.*

Tweedie 71 (BM); Rio Fósiles, *c.* 1000 m, April 1905, *P. Dusén* s.n. (FI, H, M, UPS). Tierra del Fuego: Parque Nacional Tierra del Fuego, Ushuaia, 'Weg zum' Glacier Martial, *c.* 750 m, 7 December 1973, *A. Henssen & G. Vobis* 24431a (MB); Sierra Alvear (type locality of *Neuropogon trachycarpus* f. *elatior* Lamb) 800–900 m, 7 February 1940, *R. Santesson* 639b (UPS, S), 650 m, 9 February 1940, *R. Santesson* 636b p.p. (UPS); Sierra Sorondo, N. slope, above Las Cotorras, *c.* 20 km ENE. of Ushuaia, 800 m, 6 February 1940, *R. Santesson* 641b (S, UPS); Monte Marcial, above Ushuaia, 700 m, 29 January 1940, *R. Santesson* 450b (UPS, S).
ÎS. KERGUELEN. part of type collection (BM); December 1898, *W. Schimper* (UPS).
Uncertain determination
ANTARCTIC PENINSULA. Graham Land: Adelaide I. [*c.* 67°15'S: 68°30'W], 'Reptile Ridge', Yellow Bluff, 350 m, 9 March 1981, *R. I. L. Smith* 3453 p.p. (AAS).

For further localities see lists held in BM.
HEARD IS. see Dodge & Rudolph (1955).

Appendix I. Allied taxa

Descriptions and brief notes on the following three taxa, *Usnea amblyoclada, U. inermis,* and *U. torulosa,* are appended to assist in the identification of some of the species of *Usnea* subgenus *Usnea* that can occur in communities with *Neuropogon* species and may rarely be somewhat darkly pigmented. In general, this pigmentation is scant in all three and lacks the violaceous lustre which is a characteristic of many species of *Neuropogon*; more extensive pigmentation only seems to occur in damaged or moribund specimens.

In Australasia only two species of the subgenus *Usnea, U. torulosa* and, to a lesser extent, *U. inermis*, occupy similar habitats to *Neuropogon*, both appear to virtually replace the latter subgenus in alpine habitats. They may be distinguished, particularly from species of the *U. ciliata* complex, by the development of true isidia.

A larger number of saxicolous *Usnea* species have been described from South America including a well-defined group of related species which Motyka (1938) assigned to the subsection *Roccellinae* of the *Laevigatae*. In general they are robust species, often with large amounts of usnic acid, and are rarely pigmented. Examples include *U. bogotensis*, a yellow-green species with more or less globose soralia, and the non-sorediate, fertile, *U. roccellina*, which probably form a species pair. Motyka also included the fertile species *U. amaliae* and *U. hieronymii* (and its var. *adusta*) in this subsection. However, *U. hieronymii* appears to be closely allied to, or possibly the same as, *U. densirostra*, a species which Motyka (1937) assigned to a completely different subsection, the *Densirostrae* within the section *Setulosae, U. densirostra* is the only species in this subsection which could be mistaken for a species of *Neuropogon*. This species resembles, in particular, *U. trachycarpa* in habit, but is uniformly grey-green and has a pale, not a rufous brown, apothecial disc; it also has a more northern distribution. Motyka also included *U. capensis* (South Africa), *U. amblyoclada* (South America) and *U. glomerata* (Australasia) in the same subsection. Of these species *U. amblyoclada* is possibly the sorediate counterpart of *U. hieronymii*.

Several taxa, for example *Usnea igniaria* (UPS – holotype, not seen) and *U. nidulifera* (UPS! – holotype) which are usually corticolous and only rarely saxicolous, also occasionally occur in similar, mainly upland, habitats in southern South America. These two species usually lack pigmentation and superficially resemble, but replace, *U. inermis*; both sometimes contain psoromic acid. *U. nidulifera* may sometimes be extensively pigmented (cf. *U. inermis*), but when fertile, has a pale disc (for example, Argentina, Rio Negro, Cerro Otto, 1980, herb. Kalb!).

1. **Usnea amblyoclada** (Müll. Arg.) Zahlbr. **Fig. 36**

Cat. Lich. Univ. **6**: 534 (1930). – *Usnea barbata* var. *amblyoclada* Müll. Arg. in *Flora, Jena* **72**: 509 (1889). Type: Serra Ventana, in Argentinia merid., *Lorentz* (G! – holotype; BM! – isotype). [TLC: norstictic acid, salazinic acid, usnic acid.]

Note: The combination '*Usnea amblyoclada* (Müll. Arg.) Motyka' has not formally been made (Motyka, 1937) and would be superfluous.

Description: Thallus saxicolous, rarely lignicolous, 2–3 cm, arising from a delimited, ± pigmented, holdfast, erect, richly branched above with clustered laterals and subcornute or slightly deflexed apices. Fibrils numerous, slightly articulate, often eroding. Branches terete, grey-green, rarely black-pigmented at the apices. Cortex thin, cartilagineous. Surface matt, papillate, rarely slightly inflated, then fracturing; pseudocyphellae numerous. Medulla compact or sublax, axis thick, occupying 0·5 of the branch diameter. Isidia numerous on ultimate branches and fibrils, arising from pseudocyphellae, apices black-pigmented, often eroding. Pseudoisidia and soredia absent. Apothecia and pycnidia not known. TLC: (1) norstictic acid, salazinic acid, galbinic acid, usnic acid; (2) fumaprotocetraric acid, protocetraric acid, salazinic acid, usnic acid; (3) no medullary substances, usnic acid (rare – lignicolous).

Distribution: *Usnea amblyoclada* is apparently confined to the northern part of the South America, where it is either rare or under-collected; it is recorded from Brazil, Argentina, Uruguay, and Peru (Motyka, 1937; Osorio, 1980; Swinscow & Krog, 1976). Previous reports of *U. pulvinata* from South America are assumed to refer to this taxon. Recent collections from Bolivia, Ecuador, and Peru (BM!) contain material referable to this species.

Chemistry: The primary medullary substances are norstictic acid usually with salazinic acid. In addition to type material only six collections have been examined; in these galbinic acid was found as an accessory substance in two samples. A further specimen contained salazinic, protocetraric and fumarprotocetraric acids. Lignicolous material, from Bolivia, lacked medullary substances, although norstictic acid occurred in saxicolous thalli. It is likely that other chemical races may occur and in this diversity the species would resemble *U. pulvinata* (Swinscow & Krog, 1976).

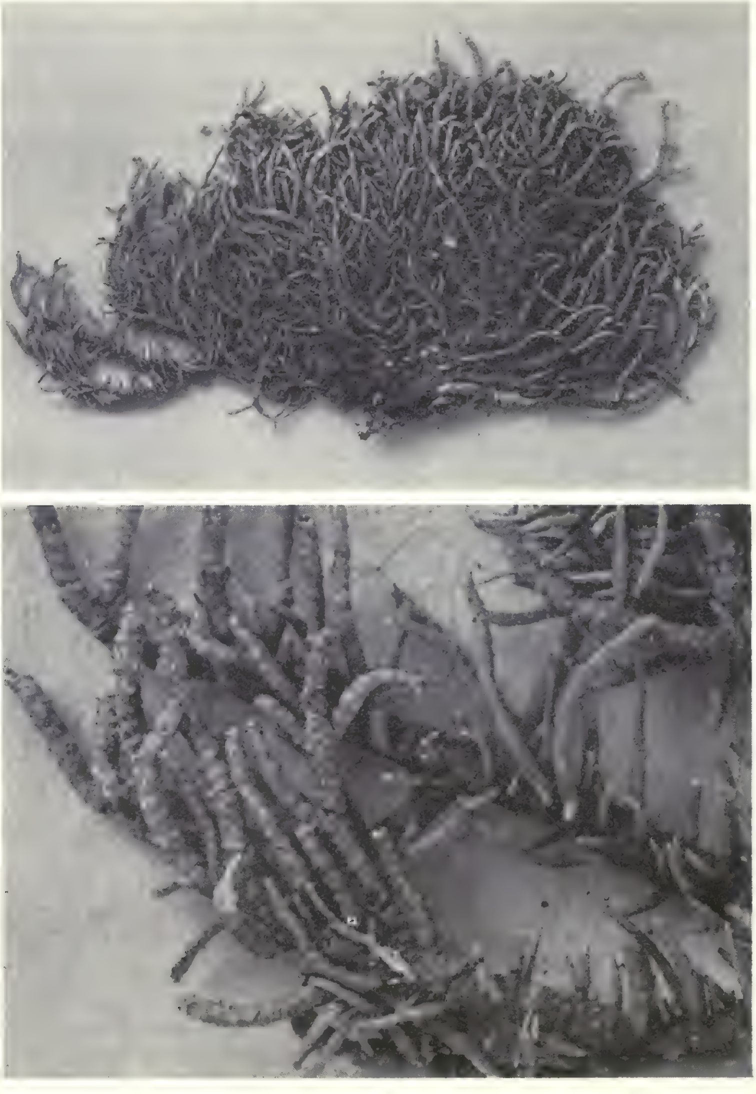


Fig. 36 *Usnea amblyoclada*. Holotype of *Usnea barbata* var. *amblyoclada* Müll. Arg. (G). Top. Whole thallus ×1. Bottom. Detail of isidia and pseudocyphellae ×10.

Discussion: The taxonomic position of this taxon remains uncertain. Swinscow & Krog (1976) initially accepted *Usnea amblyoclada* to be conspecific with *Usnea pulvinata*, although subsequently they (Swinscow & Krog, 1979) expressed some doubt about their original interpretation. I have examined the holotypes of both taxa (in G and L respectively) and, pending a more detailed study of South American and African material, prefer to regard the two taxa as distinct species, possibly in different aggregates. *U. pulvinata* belongs to the *U. bornmuelleri* aggregate which is characterised by the presence of blackened, true isidia, a cartilagineous cortex, and usually saxicolous habitat. *U. nigropapillosa*, a saxicolous endemic from Tristan da Cunha (Jørgensen, 1977), belongs to the same aggregate, and is characterised by the presence of fibrils, blackened papillae and branch apices, but lacks true isidia (O! – holotype). In contrast to *U. pulvinata, U. amblyoclada* appears to have closer affinities with *U. densirostra*, a saxicolous, fertile South American species.

Usnea amblyoclada is included here since it could occasionally be confused with *U. durietzii*. However, the former is grey-green, rather than yellow-green, has true isidia, not pseudoisidia, is more copiously fibrillate, and lacks the inflated main branches and a stalked holdfast, the features which characterise *U. durietzii*. Isidia in *U. amblyoclada* are produced extensively throughout on secondary branches and fibrils, and are not in delimited clusters as in *U. acanthella*.

2. **Usnea inermis** Motyka **Fig. 37**

Lich. Gen. Usn. Stud. Monogr. **1**: 109 (1936). Type: Australia, Victoria, ad flumen Murray, in silvis, *Wawra* (W! – holotype). [TLC: psoromic acid, 2′-O-demethylpsoromic acid, usnic acid.]

Description: Thallus corticolous, rarely saxicolous, 1–2(–5) cm, arising from a ± delimited, usually unpigmented, holdfast, erect to subpendulous, ± dichotomous to irregular, repeatedly branched above with numerous, ± subarticulate laterals and reflexed, subcornute apices. Short fibril-like branches sometimes present. Branches terete or irregular, green to yellow-green, sparsely black-pigmented at the apices. Cortex thin. Surface ± waxy, smooth to faveolate, rarely subpapillate, unpigmented annulations frequent. Medulla lax, rarely sublax, axis thin, occupying less than 0·5 of the branch diameter. Isidia frequent throughout thallus, dispersed, arising from small pseudocyphellae, ± pigmented apices, becoming extensive then confluent, often eroding. Pseudoisidia and soredia absent. Apothecia rare. TLC: (1) squamatic acid, usnic acid; (2) psoromic acid, 2′-O-demethylpsoromic acid, usnic acid; (3) no medullary substances, usnic acid.

Distribution: *Usnea inermis* is apparently confined to Australasia. In New Zealand it is characteristically a corticolous or lignicolous species, chiefly occurring at low altitudes and rarely above 600 m, although it is often as important element of the lichen flora of subalpine scrub on twigs of, for example, *Discaria* and *Leptospermum*. Similarly, in Tasmania it is primarily a corticolous or lignicolous species of dry forests from the coast up to the subalpine zone. However, in Victoria and New South Wales, *U. inermis* frequently shares saxicolous habitats with *U. torulosa* at higher altitudes, between 1500 and 2200 m.

Chemistry: Traces of an unidentified fatty acid were occasionally found in all three races. The psoromic acid race was found to be less frequent than the squamatic acid-containing race.

Discussion: *Usnea inermis* should rarely be mistaken for members of the subgenus *Neuropogon* since it has many distinguishing features, besides different ecological parameters. For example, the thallus is much greener than the majority of *Neuropogon* species, and may easily be separated from Australasian taxa by the characteristic lax medulla and randomly scattered true isidia. Thallus blackening often appears to be more prevalent in thalli growing in very exposed situations and is often the result of tissue necrosis rather than pigmentation, although a tendency to limited pigmentation at the branch apices appears to be characteristic of the species. It may be distinguished from *U. torulosa* by the laxer medulla and the dispersed, rather than delimited, isidia.

3. **Usnea torulosa** (Müll. Arg.) Zahlbr. **Fig. 38**

Cat. Lich. Univ. **6**: 594 (1930). – *Usnea dasypogoides* f. *torulosa* Müll. Arg. in *Flora, Jena* **66**: 19 (1883). Type: Mt. Koscuisko, New South Wales, *Findlay* 554 (G! – holotype). [TLC: squamatic acid, usnic acid.]

Usnea glomerata Motyka, *Lich. Gen. Usn. Stud. Monogr.* **2**: 315 (1937). Type: Nova Hollandia, saxicola, 1876, *Archer* (O – holotype, not seen).

Usnea aurescens Motyka, *Lich. Gen. Usn. Stud. Monogr.* **2**: 561 (1938). Type: New Zealand, Cave Hill, Dunedin, (*J. S. Thomson* T245) M23 (herb. Motyka – holotype, not seen, BM!, CHR 343970! – isotypes). [TLC: barbatic acid, 4-O-demethylbarbatic acid, squamatic acid, usnic acid.]

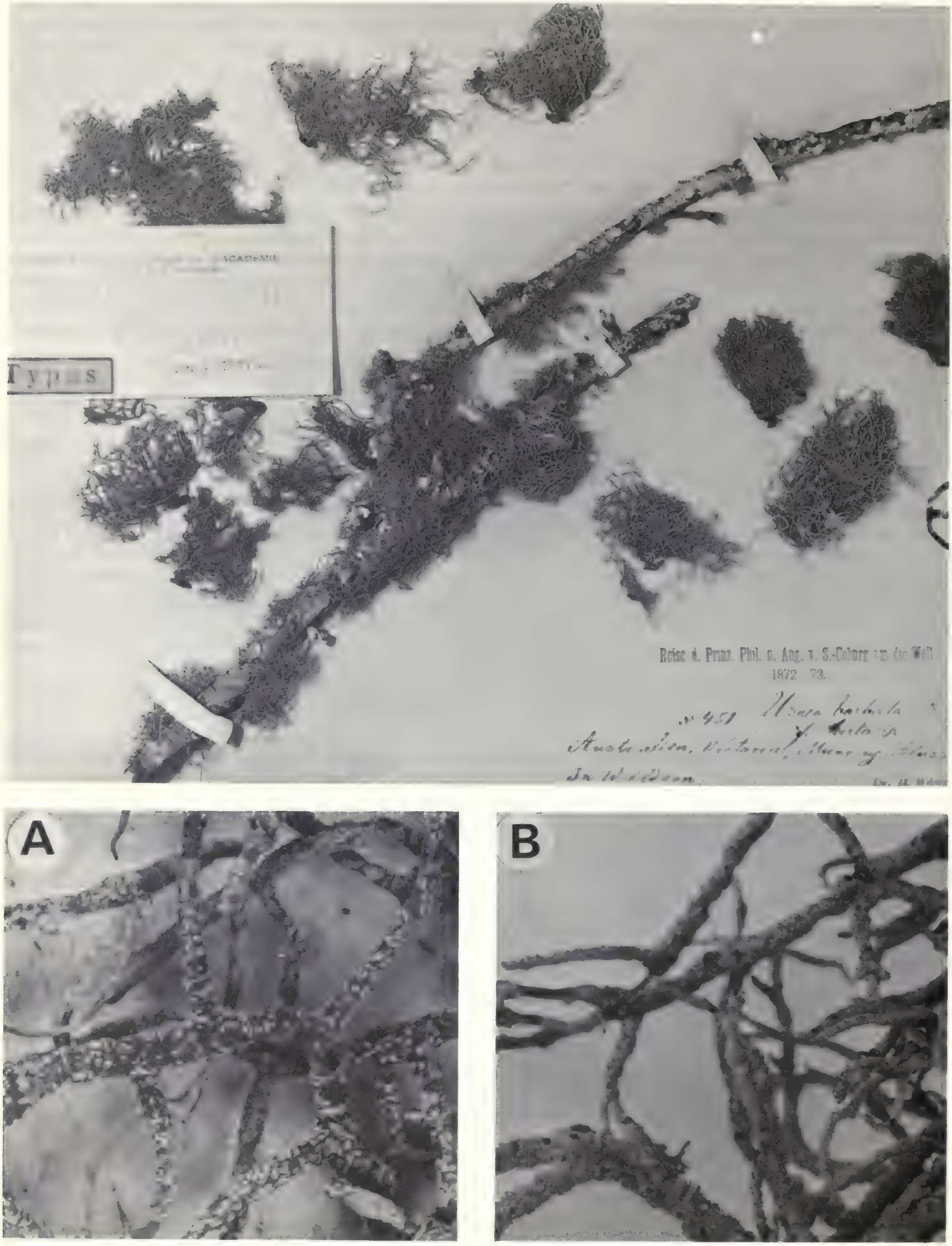

Typus
Reise d. Prinz. Phil. u. Aug. v. S.-Coburg um die Welt
1872–73.
A
B

Fig. 37 *Usnea inermis*. Top. Holotype of *Usnea inermis* Motyka (W) ×0·5. Bottom. Detail of isidia. A – holotype ×10. B – New South Wales, *Filson* (MEL 1018181) ×10.

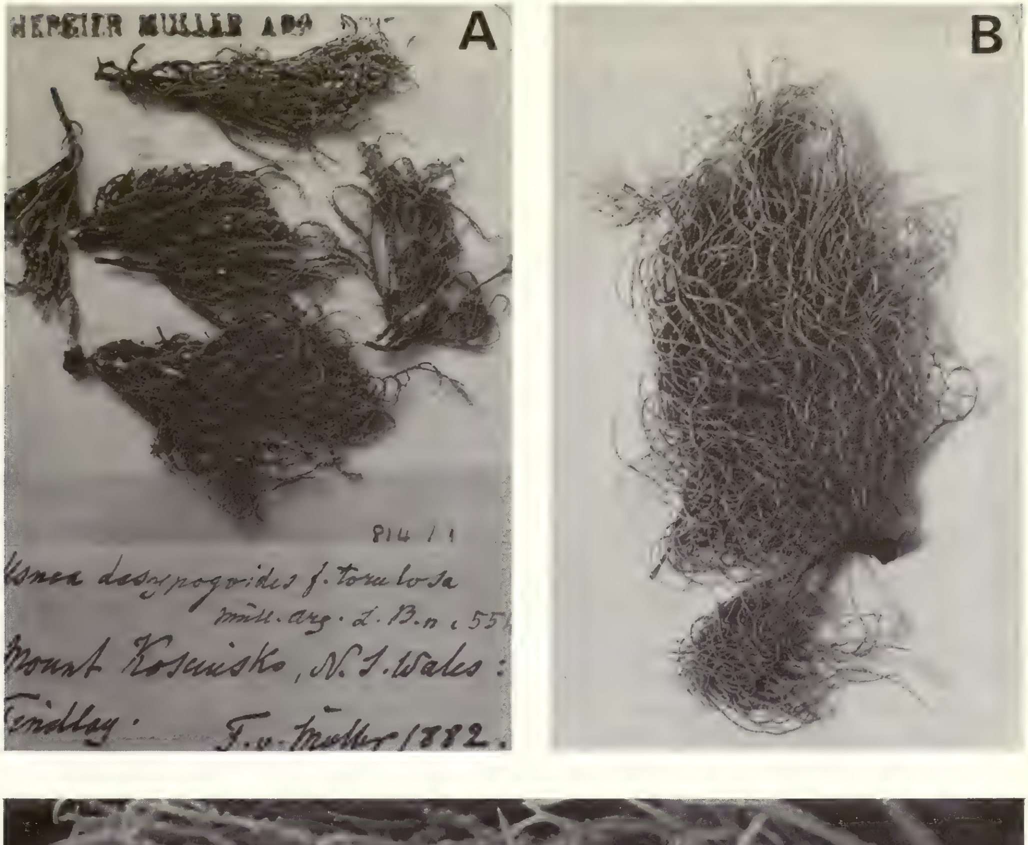

A
HERBIER MÜLLER ARG
814/1
snea dasypogoides f. torulosa
müll. arg. L. B. n. 55
ount Kosciusko, N. S. Wales :
indlay. F. v. Müller 1882.
B
C

Fig. 38 *Usnea torulosa*. A – holotype of *Usnea dasypogoides* f. *torulosa* Müll. Arg. (G) ×1. B – Isotype of *Usnea aurescens* Motyka (CHR) ×1. C – Detail of isidia. New Zealand, Otago, Old Man Range, *James* 1579 (BM) ×10.

Neuropogon acromelanus var. *inactivus* Lamb in *J. Linn. Soc.* (Bot.) **52**: 220 (1939). Type: Tasmania, Mt. Wellington, 1876, *W. Campbell*, ex herb. Stirton (BM! – holotype; BM! – isotype). [TLC: ± squamatic acid, usnic acid.]

Description: Thallus saxicolous, (3)–4–6(–8) cm, arising from a proliferating or rarely delimited, pigmented, holdfast, erect to subdecumbent, ± dichotomous, richly branched above with numerous, short, clustered, entwined laterals with capillaceous apices. Fibrils rare. Branches terete, pale yellow, unpigmented or rarely blackened at the apices. Cortex thick, rigid. Surface waxy, rarely subfaveolate or annulate, papillae absent. Medulla compact, rarely sublax, axis thick, occupying 0·5–0·6 of the branch diameter. Isidia forming ± delimited clusters, arising from minute pseudocyphellae, ± pigmented apices, often eroding to from soralia-like areas. Pseudoisidia infrequent. Soredia absent. Apothecia rare. TLC: (1) squamatic acid, usnic acid; (2) psoromic acid, 2′-O-demethylpsoromic acid, squamatic acid, usnic acid; (3) barbatic acid, 4-O-demethylbarbatic acid, ± squamatic acid, usnic acid; (4) no medullary substances, usnic acid.

Distribution: *Usnea torulosa* is widely known from saxicolous alpine or subalpine habitats in New Zealand and Australia, occurring with or sometimes replacing *Neuropogon* species. The species has a much wider ecological amplitude, and is found at lower altitudes; it is also more catholic in its choice of substrates. It seems more able to withstand competition from large foliose lichens and to tolerate some degree of nutrient enrichment, as often occurs in bird-perch communities with *Parmelia signifera. U. torulosa* also has some preference for habitats near standing water, often colonising depressions in boulders or rocks by lake sides. It also extends into areas with wetter climates, for example on the west coast of South Island, New Zealand, areas where *Neuropogon* is absent.

Chemistry: The squamatic acid containing race (Race 1) was found to be the most common, with the barbatic acid race (Race 3) being less frequent and the psoromic acid race (Race 2) rare.

Discussion: The taxonomic position of *Usnea aurescens* remains somewhat uncertain, although it is here included within the wide range of variation of *U. torulosa*. The isotype (Fig. 38) is a much less robust entity with fine, extended secondary branches with small eroded soralia-like areas that only produce a few true isidia. It is possible that some of the barbatic acid-containing specimens may eventually prove to belong to a distinct taxon. These are characterised by the presence of pronounced globular soralia-like structures which only rarely produce small pseudoisidia and appear to lack true isidia, although these entities are included within the variation of this species for the present. This probably represents another phase in the erosion-regeneration cycle of isidia production, where isidia regenerate to form pseudoisidia but ultimately erode to produce large, usually excavate, soralia-like structures.

Usnea torulosa is included in this appendix since it is frequently found associated with *U. acromelana* and might, in instances where the characteristic habit or the isidia are not well-developed, be mistaken for scantily pigmented forms of that species. In the field the two species are easily distinguished since *U. torulosa* is a much brighter yellow, in contrast to the yellow-green colour of *U. acromelana*. Pigmentation is scarce, being confined to the holdfast, isidia, and rarely the apices of secondary branches. Medullary chemistry is particularly useful in cases where identity is uncertain, since norstictic and salazinic acids, which are a feature of Australasian populations of *U. acromelana*, do not occur in *U. torulosa*.

Usnea torulosa may be distinguished from *U. inermis* by the differences in habit, branch anatomy, and, frequently, habitat. Only rarely do the isidiate areas in *U. torulosa* become confluent towards the branch apices and then resemble the random, dispersed distribution found in *U. inermis*.

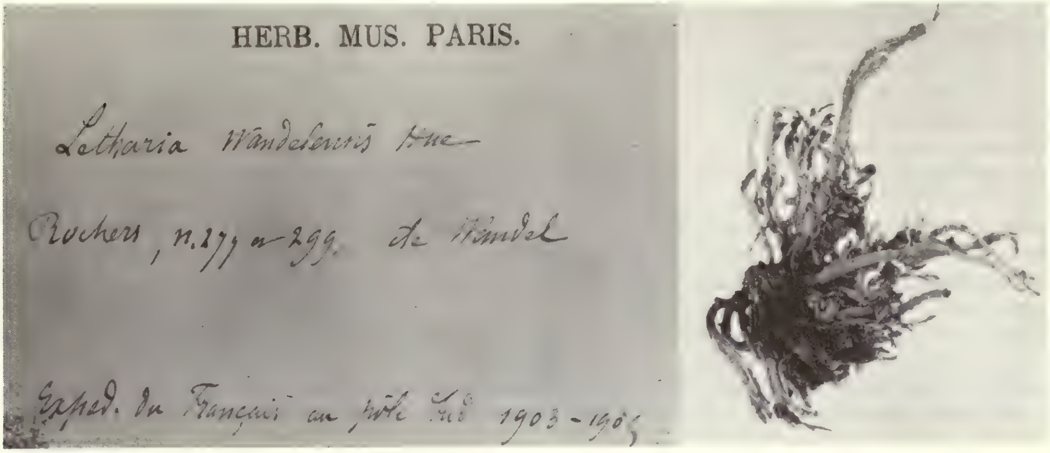
Appendix II. Excluded taxa

Letharia wandelensis Hue, *Expéd. Antarc. Franç.* 1903–1905, *Botan., Lichens:* 6 (1908). Type: Graham Land, Booth-Wandel I., *Expéd. Antarc. Franç.* 277, 299 (PC! – lectotype, selected here, CANL 16959! – isolectotype).

From the original description and examination of the type material it is obviously that this species was based on a mixture of two taxa; namely a moribund, weathered specimen of *Usnea antarctica* overgrown by, amonst other lichens, a species of *Caloplaca*. Zahlbruckner (1926) subsequently created a new genus, *Lethariopsis*, to accommodate this 'species' based on the *Caloplaca*-type spores.

Lamb (1948*b*) discussed the identity of *Letharia wandelensis* and reported that, after careful study of the apothecia, it was impossible to determine the *Caloplaca* (or *Teloschistes*) species concerned. Since Hue (1908) mentioned the occurrence of *Polycaulonia (Caloplaca) regalis* and *Polycaulonia coralligera* (i.e. *Xanthora candelaria* – Lamb, 1948*b*) as associated species, it is possible that the apothecia may belong to one of these. Lamb (1948*b*) considered the former species to be the most likely, although he also found fragments of other lichens, including a species of *Physcia*, overgrowing the thallus. Dodge (1973) retained the genus *Lethariopsis* but suggested that Lamb's interpretation was referable to *Usnea pseudofruticosa (U. antarctica)* parasitized by *Caloplaca cinericola*.

Examination of the type material (Fig. 39) shows that there is not sufficient material present to ascertain the identity of the *Caloplaca* species. Some clue to its identity may come from the parasite found in the apothecia described by Hariot (*in* Hue, 1908) as *Endococcus wandelensis*. This is a synonym of *Polycoccum rugulosarium* (Hawksworth *in* Pegler et al., 1980) which is reported from the apothecia of *Caloplaca regalis* and *Caloplaca rugulosa*. There is apparently no material of the parasite still associated with the type specimen (D. Hawksworth, pers. comm.).



HERB. MUS. PARIS.

Letharia wandelensis Hue

Rochers, n. 277 a 299. de Wandel

Exped. du Français au pôle Sud 1903-1905

Fig. 39 Type of *Letharia wandelensis* Hue (PC) ×1·5.

Under the Code (Article 9.2) the original description could adequately be used to lectotypify either the *Usnea* or the *Caloplaca* species concerned, since the taxon can no longer be rejected under Article 70. If the *Usnea* part was selected as the lectotype of *Letharia wandelensis* the name would predate *Usnea antarctica*. Consequently *Letharia wandelensis* Hue is here lectotypified on the fertile part, as an unidentified species of *Caloplaca*. This follows Recommendation 7B of the Code in selecting a lectotype so as to preserve the current usage of the epithet *'antarctica'*.

Ramalina scopulorum var. ε J. D. Hook., *Flora Antarctica* **2**: 522 (1847): Spec. orig.: dry granite rocks, Cape Horn, *J. D. Hooker* (BM!); Kerguelen's Land, *Anderson* (not traced).

Material of this unnamed variety from Îles Kerguelen was thought to be a species of *Neuropogon* (Crombie, 1879*a*; Dodge, 1948), possibly *Usnea trachycarpa*. However, examination of original material from Hermite Island, Cape Horn, *J. D. Hooker* 66 (BM!) and 76 (BM!), shows it to be *Ramalina terebrata*. It is possible that the Kerguelen specimen may have been mislabelled or misplaced, since according to Crombie (1879*a*) the genus *Ramalina* does not occur there.

Usnea barbata var. β **sulphurea** Taylor & J. D. Hook., *Flora Antarctica* **1**: 194 (1845). This taxon was described from the Auckland and Campbell Islands and, although the type has not been traced, is probably referable to *Usnea xanthopoga*. Zahlbruckner (1930: 602) gives this variety as a synonym of *U. sulphurea* (i.e. *U. sphacelata*).

Usnea cornicularia Ach., *Lich. Univ.*: 619 (1810). Type: New Zealand, *Forster* (UPS – herb. Thunberg 26348!). Zahlbruckner (1930: 601/2) cited this taxon as a synonym of *Usnea sulphurea* (i.e. *U. sphacelata*) whilst Motyka (1936) excluded it from the subgenus. The type specimen is a corticolous *Usnea*-like species of *Ramalina* (Galloway, 1985).

Usnea falklandica Motyka, *Lich. Gen. Usn. Stud. Monogr.* **2**: 472 (1937). Type: Falkland Islands, unlocalised (W – not traced). From the brief description of this species it could either represent a species of *Protousnea* or *Usnea s. lat.*, although not cited in the former by Krog (1976). Consequently this taxon may belong to the subgenus *Usnea* or even represent a scrambling form of *U. aurantiaco-atra* with scantily pigmented apices.

Usnea lutescens Stirton in *Trans. Proc. N.Z. Inst.* **30**: 388 (1898). The unlocalised type, presumably from Australasia, has not been traced in BM or GLAM. If corticolous it might be referable to *U. ciliifera* (Motyka, 1937: 544), but if saxicolous it could be *U. ciliata*, and would then become the valid name for that species.

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Cytotaxonomic studies of the ferns of Trinidad

1. The climate, geology, and vegetation of Trinidad with particular reference to the ecology of ferns

Anthony Clive Jermy

Department of Botany, British Museum (Natural History), Cromwell Road, London
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Synopsis

The topography, climate, geology, and vegetation formations found on the island of Trinidad are briefly summarised and each discussed in relation to the ecology of some of the more dominant or otherwise interesting fern species.

Introduction

Trinidad is an island in the tropical belt situated between 10°2′ and 10°50′ N. latitude and 60°55′ and 61°50′ W. longitude. The political state includes the smaller island, Tobago, 30·5 km (19 miles) NE. of Trinidad and 192 km (120 miles) SW. of Barbados. Trinidad lies close to the South American continent and Corozal Point in the north-west, together with a chain of islands, of which Chacachacare, Huevos, Monos, and Gaspar Grande are the most important, is only 11 km (7 miles) from Venezuela.

In general topography two mountain systems stretch across almost the entire island, the Northern and Southern Ranges, whilst a third, the Central Range, lies somewhat diagonally across its middle portion. The Northern Range is formed by up-folding of Upper Jurassic and Cretaceous rocks and, as such, forms the eastern extremity of the eastern branch of the Andean chain which stems from Colombia and passes through northern Venezuela. The highest points are Aripo, 925 m (3085 ft) and El Tucuche, 922 m (3072 ft). The southern uplands are relatively

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low hills, the highest being Peak 404 (304 m; 1013 ft) in the Trinité Hills; these are formed from a southern anticlinal trend or series of folds separated by a complicated fault system. It is an area that has been, at least in its western part, intensively explored for oil and very much cut over in putting down wells and pipelines, most of which are now dry and defunct. Emission of natural gases in this area gives rise to a phenomenon known as 'mud volcanoes'. Another feature in this area, at La Brea, is the Pitch Lake, covering 46 hectares (115 acres) of natural deposit of asphalt. The Central Range is another broad anticlinal uplift of Cretaceous and Eocene rocks flanked by Miocene formations, which include the prominent limestone hills of Tamana, Biche, and Brigand Hill.

Between these hills are broad synclinical depressions that in the north are bounded by a large east to west fault at the base of the Northern Range; the resulting submerged areas are now filled with Pliocene and Pleistocene deposits. In the west of this area is the extensive Caroni delta and surrounding mangrove and swamp.

Any expedition or field project that sets out with the intention of collecting a comprehensive range of a group of plants in a given area will of necessity collect ecological data, which, although often condensed on an herbarium label may not otherwise be published. The four excursions made by the author and T. G. Walker between 1963 and 1973, during which extensive collections of ferns were made and formed the basis of research reported in paper 2 (Walker, 1985), are no exception, and these short notes will hopefully give a background to the environment and provide data around which the biology of the ferns of Trinidad may be discussed.

Climatic recording in Trinidad and Tobago is not centrally organized and a variety of institutes and organisations take recordings for their own use. The data presented here are substantially taken from Berridge (1981). The major climatic controls of these islands are their latitude, their landmass size, and relative position in the ocean and to the Bermuda/Azores anticyclone, the effect of air-mass migrations (mainly the NE. and SE. Trades), and more locally the effect of topography.

The seasons display monsoonal characteristics, the dry season coinciding for the most part with the northern hemisphere winter and the wet with summer. Collecting for this project was done for the most part in that wet season July–October, although one trip was made by M. G. and T. G. Walker in April. It is interesting to note that whilst the ferns of open habitats, e.g. road banks, and epiphytes in the more exposed crowns of trees responded quickly to the increased summer rainfall in flushing and quickly sporing, those species of the forest floor took some while before the effect of the increased rainfall took effect. Even those species in the deeper, more or less constantly moist ravines appeared to exhibit seasonality in spore production.

Climate

Rainfall

Trinidad's annual rainfall totals vary from over 3048 mm (120 in) in the NE. to approximately 1524 mm (60 in) in the NW. and SW. peninsulas (see Fig. 1) and are related to the topography and upwind location in the local precipitation regime. The difference in amounts between the wet and dry season is considerable, the wet season maps showing a distribution from 2032 mm (80 in) to 635 mm (25 in), and the dry season from 1016 mm (40 in) to 254 mm (10 in). Tobago exhibits the same patterns differing only in amounts. Table 1 gives the mean monthly rainfall and Table 2 the mean number of days in each month when less than 1 mm of rain fell.

Diurnal variation is more marked than might be expected in the small landmass. There is a tendency for midday and early afternoon showers inland. On the east coast convergence of air masses from land and sea regularly give showers in the evening and night. The intensity of rain is greater in the wet season. Topography will influence local convection currents, and a few areas of the higher ground will get almost daily rain throughout the year.

Table 1 Mean monthly rainfall (in mm). Based on Piarco records after Berridge (1981).

Jan.	Feb.	Mar.	Apr.	May	June
80·9	50·6	33·6	50·9	118·7	262·3
July	Aug.	Sept.	Oct.	Nov.	Dec.
254·1	247·0	180·4	160·8	206·6	150·0

Table 2 Mean number of days in each month with rainfall of less than 1 millimetre. Based on Piarco records after Berridge (1981).

J	F	M	A	M	J	J	A	S	O	N	D
20	19	25	23	19	10	11	12	15	15	13	16

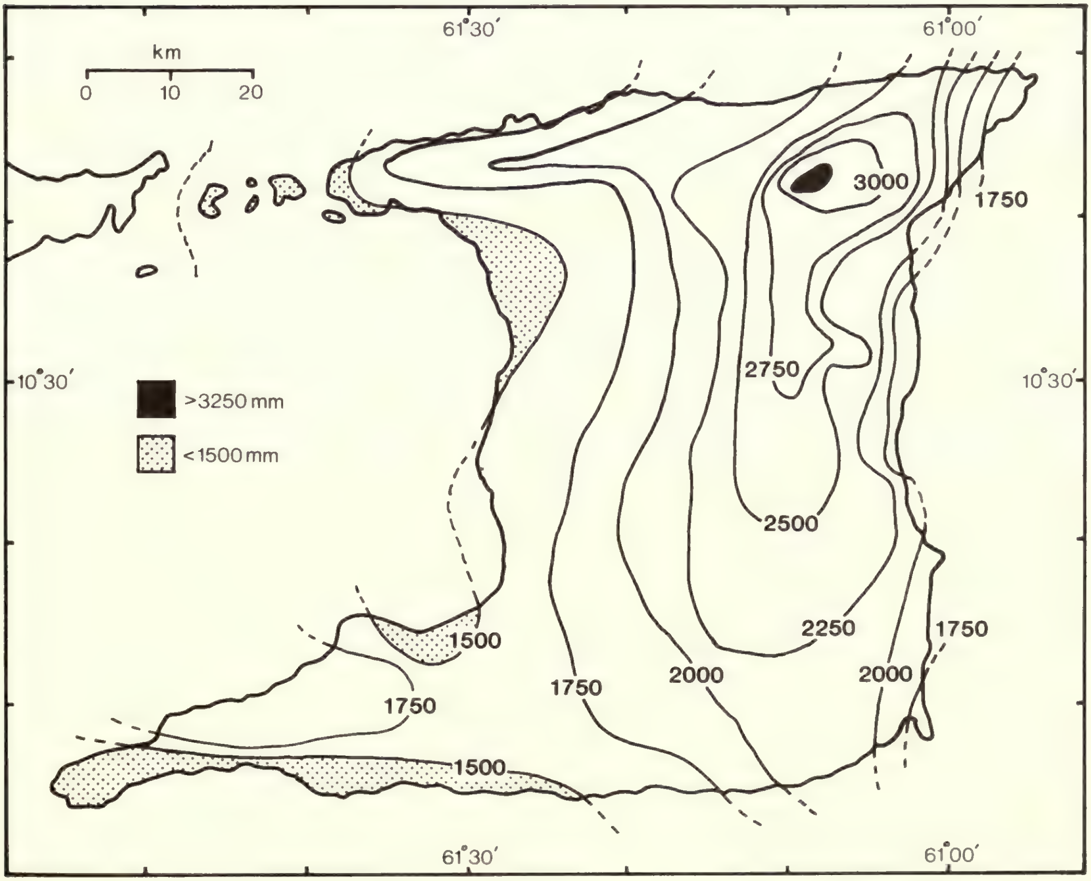
61°30′
61°00′
km
0
10
20
10°30′
10°30′
>3250 mm
<1500 mm
3000
1750
2750
2500
2250
2000
1750
2000
1750
1500
1750
1500
61°30′
61°00′

Fig. 1 Isohyetal map of mean annual rainfall recorded over 30 years (1939–1968). (Adapted from Berridge, 1981.)

Table 3 Monthly mean (dry bulb) and means of maximum and minimum temperatures (in °C). Based on Piarco records after Berridge (1981).

	J	F	M	A	M	J	J	A	S	O	N	D
Monthly mean	24·5	24·7	25·3	26·2	26·6	26·1	26·0	26·1	26·2	26·1	25·5	24·9
Mean minimum	20·4	20·4	20·9	21·9	22·9	23·1	22·7	22·6	22·6	22·5	22·0	21·2
Mean maximum	30·6	30·3	31·1	31·8	31·6	30·6	30·7	31·0	31·4	31·3	30·7	30·0

Temperature

Such is the effect of the Caribbean Sea and the Atlantic Ocean on the temperatures of Trinidad that the seasonal variation is only about 2–3°C in the mean (see Table 3). Diurnally the variations are greater – approximately 10–15°C between night and day. The mountain ridges, in the Northern Ranges at least, are high enough to show some decrease in temperature with altitude which in turn affects the vegetation and the plants which grow in this situation.

Humidity

For most of the island humidities are high throughout the year, and the relative humidity (i.e. the percentage rates of actual water vapour in the atmosphere for a given temperature against its total saturated capacity) lies in the region of 80%, with extremes from almost 100% to 50%. Even the air close to roadside or river banks in the open may be quite humid due to evaporation from seepage water or vegetation and as such forms excellent conditions for prothalli and young sporophyte growth.

Winds

Wind is a highly variable parameter, influenced by local effects of topography, land heating, etc. Berridge (1981) stresses that extra local records might give a more accurate picture of the variation of wind direction, which is biologically of greater significance than the traditional impression of dominant westerlies in the dry season and strong easterlies during the wet. Berridge has frequently recorded surface winds from the west in both seasons, and also from the south, south-west, north, and north-west in the Gulf of Paria. Such winds could be effective in dispersing spores and establishing species from both the South American mainland and the Lesser Antilles.

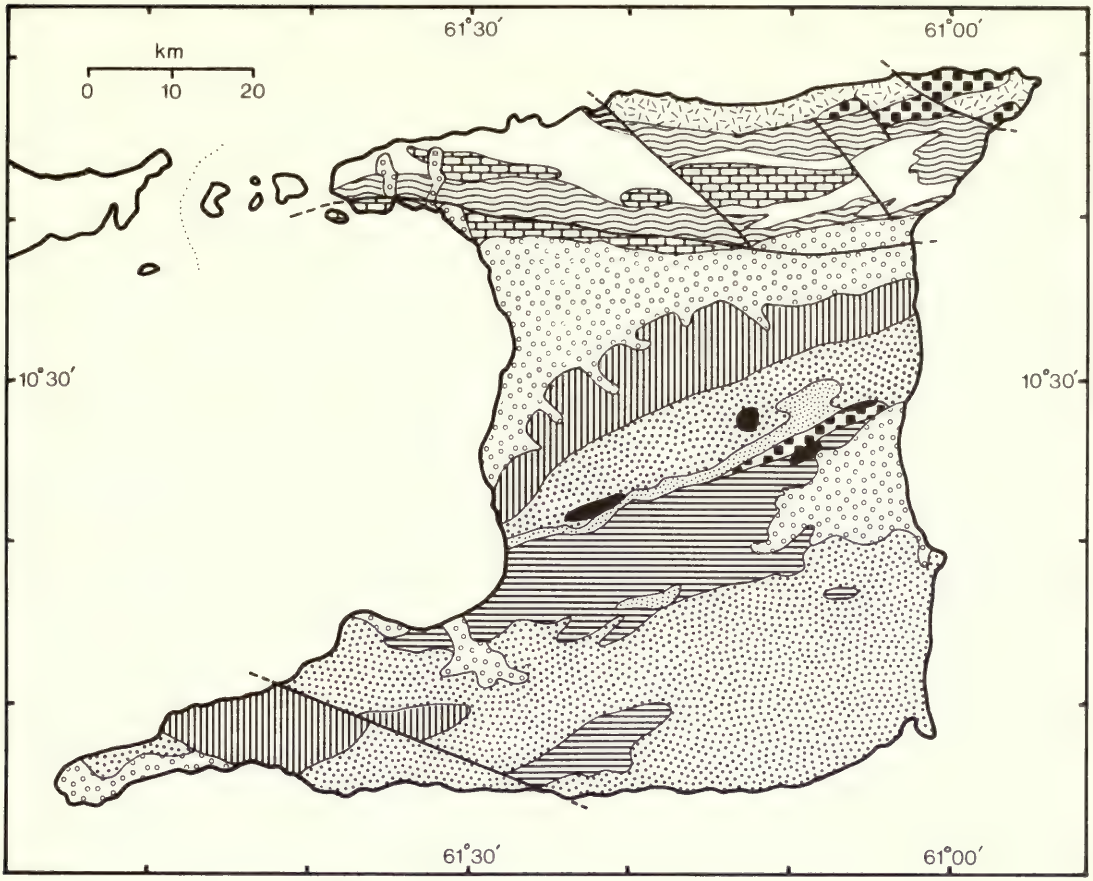

Fig. 2 Geological map of Trinidad. (Modified from Kugler, 1959.)

□ ▤ } Jurassic/quartz-mica schists, quartzites, and phyllites

▩ Cretaceous andesite

≋ phyllitic shales

▨ grits with volcanic tuffs

░ Eocene and Paleocene chalky marls

▤ Oligocene marls and clays

▒ ■ } Miocene glauconitic and calcareous sands and limestones

▥ Pliocene clays, silts, and sands

◌ Pleistocene silty terraces

Geology and soils

Solid geology

Trinidad is geologically part of the South American plate which in Jurassic/Cretaceous times (*c.* 130 million years ago) was moving away from Africa upon the splitting up of Gondwanaland. Orogenic movements that uplifted the sandstone hills of Roraima, the eastern Venezuelan mountains, and the Trinidadian Northern Ranges in turn lowered the coast areas and Orinoco basin, which became filled with later deposits, mainly calcareous clays and silts and, to a lesser extent, sands. The geology consists of a series of metamorphic rocks (slatey phyllites with subordinate limestones, quartzite, and grits) of Upper Jurassic origin, with Cretaceous shales and siltstones (Fig. 2). The limestone valleys and sinkholes of the Guanapo Heights are particularly rich in ferns, and large cave systems are found at Gaspara, Aripo, and Oropuche. In the north-east near Sans Souci is the only intrusion of volcanic rocks seen in the island, an intrusion that partially metamorphosed the adjacent rocks.

A broad anticlinal uplift was pushed up in late Miocene times with strong folding from Pointe-a-Pierre through Tabaquite to Mount Harris, Tamana, and Brigand Hill where often rubbly limestones are exposed. The southern shoulder of this uplift, around Naparima Hill exposes, amidst faults and folds, the Cretaceous core of hard siliceous siltstone. Thus, here, as in the Northern Ranges, juxtaposition of acid and basic rocks exists.

The southern uplands, low altitude hills stretching from Palo Seco to Guayaquayare form the southern anticlinal trend. Its highest peak lies in the Trinité Hills and again contains many fractures and faults giving interbedded sands, silts, and clays as mentioned above, with occasional chalky marls and limestones. An interesting feature of this district is the occurrence of mud volcanoes where silty mud flows or periodically 'erupts' through conical vents due to pressures exerted by natural gas escaping along fault fractures. They are in no way connected with normal volcanic action, but are ecologically significant in that they form areas of fine silt ready to be colonised by seedlings and in damper areas by prothalli, in what would otherwise be a closed grassland or scrub community.

The intervening lowland between these folds was filled with sands, gravels, and alluvium in Pleistocene times. Superimposed on this geology is an erosion pattern of drainage systems involving six major rivers: Caroni, Oropuche (northern), Guaracara, Nariva, Oropuche (southern), and Ortoire. Many smaller streams drain the northern flanks of the Northern Range and the southern edge of the southern hills. Within the Caroni and northern Oropuche systems, are highly productive agricultural areas interspersed with river terraces, one of which is ecologically important, the Aripo Savanna. The estuaries of these rivers, and especially the Nariva, contain swamps and tidal mangroves.

Soils

The soils of Trinidad have been discussed by Hardy (1981), and the reader is referred to that paper for details. Seventy-eight soil types are described for Trinidad by Chenery (1952) and other soil surveyors. Six major sub-divisions are used in mapping and a simplified map is given here (Fig. 3) from Hardy (1981). The *Highland Upland* soils all occur on sloping land and are all free draining sands, loams and loamy clays usually developed on fine-grained metamorphic sediments, limestone, and sub-basic igneous rock. They are all restricted to the Northern Range where the drainage is almost entirely by few, south-flowing rivers partly filled with alluvium.

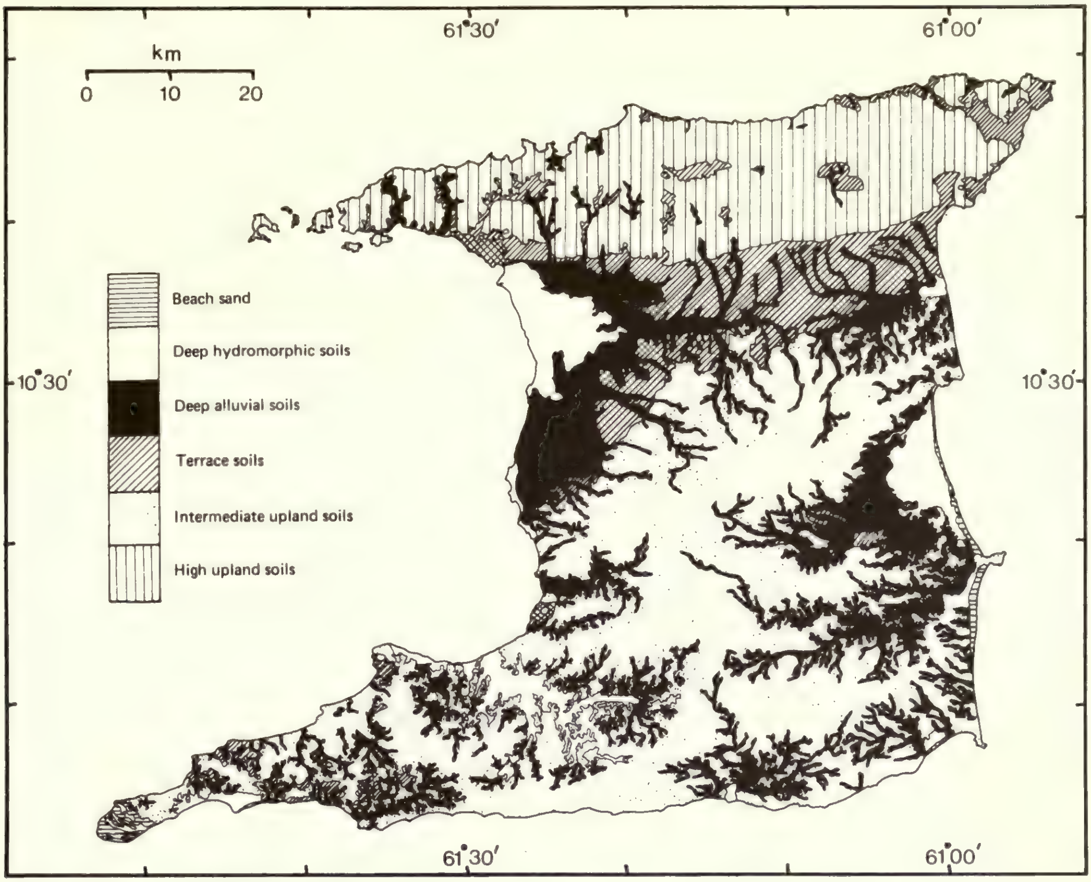
61°30′
61°00′
km
0
10
20
Beach sand
Deep hydromorphic soils
Deep alluvial soils
Terrace soils
Intermediate upland soils
High upland soils
10°30′
10°30′
61°30′
61°00′

Fig. 3 Simplified soils map of Trinidad. (From Hardy, 1981, with permission of Edward Arnold.)

The *Intermediate Upland* soils are those seen in the hills of the centre and the rolling country in the south. Mainly they are clays with occasional sandy clay-loams and loamy fine sands. Terrace soils range from gravelly sandy clay-loam, sands such as at Aripo Savanna and fine sandy loams to clays. The deep alluvial soils are again clays predominantly, and sandy clay-loams. Whilst much of this area (28% of the country) is under agriculture it is along river banks and on such nutrient-rich soils that much of the fern flora may be found. This may not be due solely to the soil type but also to the availability of water and light where watercourses make a break in forest canopy.

The *Deep Hydromorphic* soils are to be found in the Caroni and Nariva delta regions where the drainage is impeded and the fern flora of such areas restricted to swamp species (see p. 144).

Vegetation

Beard (1946) was the first to describe in any detail the natural vegetation of Trinidad and, two years before, of Tobago (Beard, 1944). The main factor controlling vegetation formations in the tropics is humidity/water availability, although tree species composition may be largely influenced by the chemical or physical nature of the soil or substrate. The same may be said for ferns and other pteridophytes, the majority of which have adapted themselves to low light intensities by having a low photosynthetic compensation point, as high humidity is most frequently associated with shady gullies and under dense canopy. A number of species in all groups are, however, adapted for other more exposed situations (mountain tops, landslips, road banks, savanna, and open scrub).

The vegetation of Trinidad and Tobago consists of 45% (by area) of forest formations of various kinds either in state or private ownership. Of this area 25·6% of the total land area (129,968 ha; 324,920 acres) are legally proclaimed Forest Reserves, with the intention of them remaining under forest in perpetuity (Chalmers, 1981), the rest being other kinds of state-owned or private forests. The majority of the Forest Reserves are in the east and south-east seasonal lowland areas with very small areas in the ever-wet montane region of the Northern Range. Trinidad still lacks a comprehensive system of nature reserves to conserve representative examples of all natural forest formations. Of the remaining 55% of land surface, some 50% is, or has been, put over to agricultural use since the European colonisation of 1532. In the lowlands smallholdings or larger estates and plantations are still maintained, but many areas in lower montane forest once planted with cocoa have reverted to secondary forests or shifting cultivation. They can be an interesting habitat for ferns.

The ecological characteristics of Beard's six major categories of vegetation formation are discussed in relation to the biology of some of the ferns found there.

Seasonal (lowland) rain-forest formations

Beard (1946) divided these into three associations: (a) evergreen seasonal forest; (b) semi-evergreen seasonal forest; and (c) deciduous seasonal forest. Seasonal formations compose almost the whole of the remaining forest (excluding plantations of teak and pine) in the lowland centre and south of the island. The distribution of rainfall is thus important, those areas with a higher rainfall producing evergreen forest and the lower rainfall deciduous. Other factors such as the degree of slope, porosity, or water retention capabilities of the soil/country rock must also be considered. Thus the forest up to 300 m on the steeper Central Range mountain slopes on shallow skeletal soils over limestone gives not an evergreen but a semi-deciduous forest type.

The evergreen seasonal forest is in areas with over 1778 mm (70 in) annual rainfall, with an average of three months each with under 102 mm (4 in) rain but over 51 mm (2 in). Beard calls this forest the *Carapa guianensis – Eschweilera subglandulosa* association and described five facies of which the Mora forest is the most distinctive, *Mora excelsa* Benth. being often 60% of the standing crop.

Ferns are conspicuous in such untouched or dense forest. On the ground *Adiantum obliquum* Willd., *A. latifolium* Lam., *A. pulverulentum* L., *Asplenium abcissum* Willd., *A. salicifolium* L., *Cyclopeltis semicordata* (Swartz) J.Sm., *Danaea nodosa* (L.) Sm., *Diplazium grandifolium* (Swartz) Swartz, *Pteris tripartita* Swartz, *Rumohra adiantiformis* (Forst.) Ching may be frequent. Above this herb layer at 12–27 m is an almost continuous canopy with occasional emergents rising to 30 m. Epiphytes are few on these emergent branches. *Asplenium serratum* L., *Dicranoglossum desveauxii* (Klotzsch) Proctor, *Oleandra articulata* (Swartz) C. Presl, *Polypodium ciliatum* Willd., *P. polypodioides* (L.) Watt, *Vittaria lineata* (L.) Sm. are recorded on fallen trees or on lower trees near watercourses. On the boles of trees are *Campyloneurum* spp., *Lomariopsis marginata* Kuhn, and *Polybotrya caudata* Kunze.

In the dry period many of these epiphytes will show signs of stress and obviously wilt, only to be revived on wetting. Some species show special adaptation, such as *Polypodium polypodioides*, in which the fronds are densely covered with overlapping scales and in which the frond itself curls up in drought conditions, thus conserving water.

Much of the seasonal forest has been cut over, and in the more open glades amongst stands of *Curculigo scorzonerifolia* (Lam.) Baker, *Cyathea microdonta* (Desv.) Domin, and *Trimezia martinicensis* (Jacq.) Kunth, are thelypterids like *Christella dentata* (Forssk.) Brownsey & Jermy, *Goniopteris megalodus* C. Presl, and *G. paucijuga* (Klotzsch) Pichi-Serm. *G. poiteana* (Bory) Ching, *G. tetragona* (Swartz) C. Presl, and *Meniscium nesioticum* (Maxon & Morton) Jermy & T. Walker occur especially along trackways and by streams, with *Fimbristylis* spp., *Torulinium odoratum* (L.) Hooper, *Pityrogramma calomelanos* (L.) Link, *Selaginella broadwayii* Hieron., and *Tectaria incisa* agg., including *T.* × *bulbifera* Jermy & T. Walker and *T. vivipara* Jermy & T. Walker.

Epiphytes in the more open forest compete with bromeliads, but *Ananthacorus angustifolius* (Swartz) L. Underw. & Maxon, *Polypodium ciliatum*, *P. crassifolium* L., *P. phyllitidis* L., and *Polytaenium feei* (Schaffner ex Fée) Maxon may be found on the smaller branches especially near river courses where light increases. *Didymoglossum angustifrons* Fée, *D. krausii* (Hook. & Grev.) C. Presl, *D. punctatum* (Poiret) Desv., *D. pusillum* Swartz, and *Microgonium kapplerianum* (Sturm) Pichi-Serm. are occasional on larger boles, but rarely together on the same tree.

Semi-deciduous forest areas have the equivalent of five months each with under 1000 mm (40 in) of rain but over 25 mm (1 in). The annual precipitation is 1250–1750 mm. Beard gives two associations depending on rainfall and soil type. They are to be found along the north coast and down the east of the island, becoming the dominant forest type on steeper slopes of the southern hills. They were only briefly visited by the present author. Lianes appeared to be very conspicuous and bromeliads common on the larger trees both on limbs and trunks; other epiphytes, especially ferns and mosses, were almost absent. One facies of the *Trichilia–Brosimum* association, that containing a substantial amount of *Ficus tobagensis* Urb. and *Cedrela odorata* Roemer, is seen on the well drained skeletal soils over limestone at Tamana, Brigand Hill, and Cumaca. Here the fern flora increases in the upper parts of these mountains with *Adiantum* spp., *Asplenium* spp., *Danaea nodosum* (L.) Sm., *Diplazium cristatum* agg., and *Tectaria* spp. (especially *T. purdiei* (Jenman) Maxon).

Deciduous seasonal forest lies in areas with 750–1250 mm (30–50 in) of rain per year and with the equivalent of five months with less than 100 mm (4 in) rain each of which two months have under 25 mm (1 in). The formation has a highly discontinuous emergent layer at 12–18 m and an almost continuous layer at 3–10 m. The forest has suffered considerably from human activities. It is to be found on the islands of the NW. peninsula and on the peninsula itself on foothills of the western end of the Northern Range. Epiphytes are virtually absent, although *Polypodium aureum* L. may be common especially in littoral situations.

Dry evergreen forest

Coccoloba scrub and *Roystonea* palm associations are generally termed littoral woodland. These are limited to near the sea on the east coast and have not been studied floristically as far as ferns are concerned. It may be noted here however that *Cyclosorus interrupta* (Willd.) H. Itô is common in the short herb layer underneath coastal coconut palm estates. Normally this is a swamp or ditch species and it must be able to tolerate considerable salt in the strong winds; it has a tough leathery leaf tissue.

Montane formations

The terminology of the altitudinal zones (formations) of this rain forest follows Beard (1946), although in comparison with S.E. Asia for instance, Beard's Lower Montane Rain Forest, at an altitudinal range of 250–750 m (Fig. 4), would be included in a lowland forest zone by Whitmore (1975).

Lower montane forest is restricted to the Northern Range in an area receiving 1875–3750 mm (75–150 in) of rain per year, evenly distributed. For the most part these forests are over schists, although where they are on skeletal soils over limestone Beard (l.c.) calls them seasonal montane forest, claiming subsoil drainage is so free that it is depressed to the point of seasonal drought. The structure, life-form, and flora are intermediate between lower montane forest and the seasonal evergreen forest described above. Beard gives the following as generally diagnostic of this type of rain-forest: *Byrsonima spicata* (Cav.) Rich., *Licania biglandulosa* Griseb., *L. ternatensis* Hook. f., and *Sterculia caribaea* R.Br.

The boles of the trees are never excessively large, being, on average, around 2 m in girth. They are unbranched for 12 m before opening to a narrow crown, which forms a closed canopy between 20 and 30 m. On the larger boles pyrenocarp lichens cover large areas. Small Hymenophyllaceae, e.g. *Didymoglossum* and *Microgonium* species are commonly adpressed to the smooth bark. Epiphytes are relatively few, being on the larger branches; bromeliads such as *Tillandsia* and *Vriesia*, and aroids are dominant, and ferns like *Asplenium serratum* L., *Campyloneurum* ssp., *Polybotrya* spp., and *Salpichlaena volubilis* (Kaulf.) J.Sm. are frequent.

The ground flora of Marantaceae and Zingiberaceae is otherwise predominantly of ferns, frequently many individuals of the same species covering many square metres. This dominance is seen in *Cyclopeltis semicordata* (Swartz) J.Sm., *Tectaria purdiei*, and several *Adiantum* spp., e.g. *A. tetraphyllum* Humb. & Bonpl. ex Willd. and *A. villosum* L., especially on deeper loamy soils in the lower foothills. Furthermore, species assemblages often change drastically in the next hollow of the hill, suggesting that spore dispersal does not reach very far. At or just above ground level in these denser forests the air movement must be nearly nil.

In the deeper forest the herb layer includes *Adiantum obliquum* Willd., *A. pulverulentum* L., and *A. serratodentatum* Willd., *Dennstaedtia adiantoides* (Humb. & Bonpl. ex Willd.) T. Moore, *D. ordinata* (Kaulf.) T. Moore, *Diplazium cristatum* (Desv.) Alston, *D. grandifolium* (Swartz) Swartz, *D. striatum* (L.) C. Presl, *Metaxya rostrata* (Kunth) C. Presl, *Pteris arborea* L., *P. inaequalis* (Fée) Jenman, and *Tectaria incisa* Cav. The paths (traces) through this forest often result in moist clay vertical banks in shade which make an excellent nursery for prothalli and sporelings of many genera, e.g. *Blechnum* (especially *B. fraxineum* Willd. and *B. occidentale* L.), *Cyathea, Metaxya, Salpichlaena* and *Selaginella. Gleichenia* may also germinate but lack of light prohibits any substantial growth.

Montane rain-forest is defined by Beard (l.c.) as those limited areas on the Northern Range above 750 m (see Fig. 4), mostly on the Aripo Massif. The rainfall is estimated as around 5000 mm (200 in) well distributed throughout the year, and for much of the latter part of the day and during the night cloud or mist covers the area. The average temperatures lie between 15·5° and 21°C. There is a general transition zone to the lower montane, stretching down especially along the ridges to 540 m, where *Richeria* and *Eschweilera trinitensis* A. C. Smith & J. S. Beard, such characteristic species of the montane forest, are joined in equal dominance by *Licania biglandulosa*.

The canopy is closed at 15–19 m and few trees exceed 1·5 m girth. There is a lower storey of small trees with a number of palms and tree ferns, many of which grow where a wind-break through the canopy occurs. Both lianes and epiphytes are luxuriant, with *Carludovica*, aroids, bromeliads, and orchids, and with many ferns, especially Hymenophyllaceae (*Mecodium polyanthos* (Swartz) Copel., *Sphaerocionium hirsutum* (L.) C. Presl, *Trichomanes arbuscula* Desv., *Vandenboschia hymenophylloides* (Bosch) Copel.) and *Asplenium serra* Langsd. & Fischer, *Cochlidium linearifolia* (Desv.) Maxon, *Dicranoglossum desveauxii, D. polypodioides* (Hook.) Lellinger, *Elaphoglossum lingua* (Raddi) Brackenr., *E. longifolium* (Jacquin) J.Sm., *E. undulatum* (Willd.) T. Moore, *Lycopodium aqualupianum* Spring, *L. linifolium* L., *Polypodium astrolepis* Liebm., *P. ciliatum, P. nematorhizon* Eaton, *P. pectinatum* L., *Polytaenium feei*, and *Xiphopteris serrulata* (Swartz) Kaulf. Climbing into the canopy especially on the ridges are *Oleandra articulata, O. trinitense* Maxon, *Polybotrya caudata*, and *P. cervina* (L.) Kaulf.

On the ground and in denser vegetation, gullies, and similar niches the following are locally abundant, especially on Aripo and El Tucuche: *Asplenium macilentum* Kunze ex Klotzsch, *Ctenitis aripensis* (C. Chr. & Maxon) Lellinger, *C. tucuchensis* Jermy & T. Walker, *Didymochlaena truncatula* (Swartz) J.Sm., *Diplazium caracasanum* (Willd.) Kunze, *D. centripetale* (Baker) Maxon, *Goniophlebium nephrodioides* (Klotzsch) Proctor, *Hemidictyum marginatum* (L.) C. Presl, *Hypoderris brownii* Hook., *Lindsaea lancea* (L.) Bedd., *Pteris inaequalis* (Fée) Jenman, *Saccoloma inaequale* (Kunze) Mett., and *Tectaria incisa.* On banks in the shade are *Davalliopsis elegans* (L. C. Rich.) Copel., *Feea osmundoides* (DC.) Copel., *Lecanolepis membranaceum* (C. Presl) Pichi-Serm., and *Selenodesmium rigidum* (Swartz) Copel., with *Selaginella cladorrhizans* A.Braun, *S. porelloides* (Lam.) Spring, and *Lycopodiella cernua* (L.) Pichi-Serm. in more open areas. In the upper reaches of montane forest, tree ferns often increase and *Cyathea aspera* (L.) Swartz, *C. sagittifolia* (Hook.) Domin, *C. spectabilis* (Kunze) Domin, and *C. surinamensis* (Miq.) Domin are common. On the summit of El Tucuche *Lophosoria quadripinnata* (Gmel.) C. Chr. is rare but well established in association with *Gleichenia brittonii* (Maxon) C. Chr.

Elfin woodland is a thicket formation of tree ferns, palms, and *Clusia intertexta* Britt., with a few other small tree species, reported by Beard from El Aripo, from 840 m to its summit of 925 m. Signs of similar vegetation were also seen by the author on the west ridge of El Tucuche. Trees attain heights of 6–7·5 m, *c.* 30 cm girth, and emerge from the dense layer of tree ferns (*Cyathea caribaea* Jenman and *C. tenera* (Hook.) T. Moore) and palms (*Euterpe broadwayana* Becc. and *Prestoea pubigera* Nicholson). The ground layer is virtually bare. The tree stems, branches, and twigs are covered with mosses and lichens, and occasional Hymenophyllaceae (e.g. *Sphaerocionium hirsutum*) and Grammitidaceae.

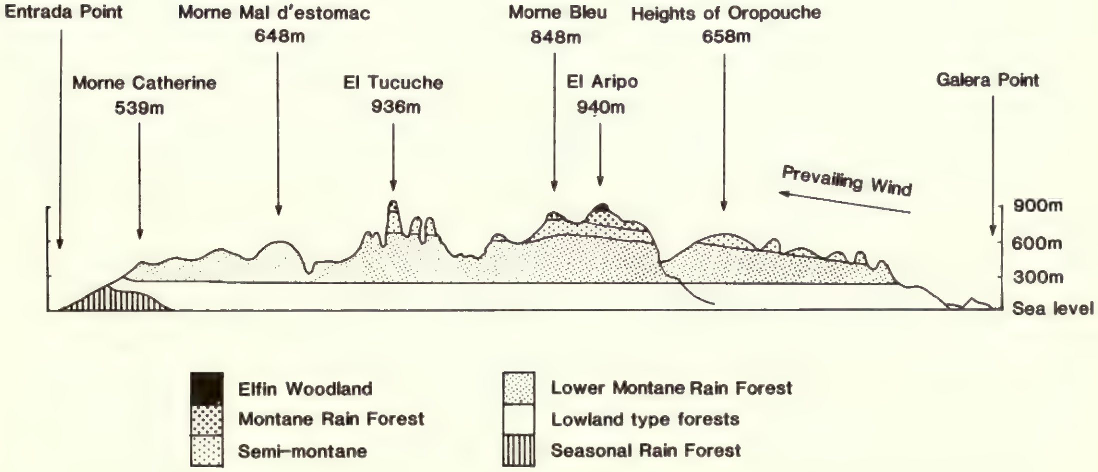
Entrada Point
Morne Mal d'estomac 648m
Morne Catherine 539m
El Tucuche 936m
Morne Bleu 848m
El Aripo 940m
Heights of Oropouche 658m
Galera Point
Prevailing Wind
900m
600m
300m
Sea level
Elfin Woodland
Montane Rain Forest
Semi-montane
Lower Montane Rain Forest
Lowland type forests
Seasonal Rain Forest

Fig. 4 Diagrammatic section E–W along the Northern Ranges, Trinidad, indicating the altitudinal distribution of vegetation formations. (Adapted from Beard, 1946.) There is a considerable intergrading of lower montane and montane forest, here called 'semi-montane'.

Swamp communities

Several swamp communities were described by Beard; there are, however, few ferns associated with them.

The *palm swamps* near Omega Island in the Nariva delta in the east are characterised by *Roystonea oleracea* (Jacquin) Cook on the seaward edge, and *Mauritia flexuosa* L.fil. on the landward side. *Acrostichum aureum* L. may be associated with the former, especially where this abuts on to mangrove swamp.

Mangrove swamps (woodland), mainly *Avicennia-Laguncularia-Rhizophora*, are scattered around the coast and occasionally contain plants of *Acrostichum aureum*. On the inland side, and on or around alluvial lagoons, herbaceous swamps occur, especially at Caroni, Nariva, Roussillac, and Icacos. A main component is *Cyperus giganteus* Vahl, forming dense stands up to 3·6 m high, with *Montrichardia aborescens* Schott and floating *Leersia hexandra* frequent; *Acrostichum* species, usually *A. danaeifolium* Langsd. & Fischer, can form very large stools over 1·5 m across. *A. danaeifolium* is much more tolerant of edaphic conditions than is *A. aureum* and Adams & Tomlinson (1979) note that in Florida the former species extends inland from saline mangrove conditions, just as it does on Aripo Savanna in Trinidad, to fresh-water swamps, often in sink-holes in hammocks and in disturbed marl sites; in contrast *A. aureum* appears to be confined to coastal mangrove swamps. Proctor (1977) also comments that *A. danaeifolium* in the Lesser Antilles sometimes occurs near freshwater streams not near the sea, and Stolze (1981) records it up to an elevation of 1200 m in Guatemala.

Blechnum serrulatum L. C. Rich. is another dominant fern in these swamps and in more inland marshes, e.g. pools in savannas. In keeping with its swamp habitat, the species is abundantly supplied with aerenchyma in the rhizome and stipe, although this is lacking in the root and rachis. A feature which, as far as is known is unique (David Cutler, pers. comm.) is the presence of abundant microscopic hairs on the outsides of the cell walls which line the intercellular spaces. These may best be seen in the aerenchyma but are not wholly confined there, also being prominent in the intercellular spaces of the mid-rachis which lacks aerenchyma. The individual hairs are 3–6 μm long and form a dense coating (Walker, in prep.); their function is unknown. Growth in this species is seasonal, taking place at the onset of the wet season. The Aripo Savanna populations inhabit many of the 'islands' in the savanna and these are often subjected to burning. A plant was gathered which was on burnt-over ground and was producing new fronds, despite many of the growing points of the branching rhizome having been burnt and parts of the rhizome being extensively charred. It may be surmised that *B. serrulatum* requires the stimulus of a dry period to produce fertile fronds, since at both Newcastle and Kew where plants have been in cultivation for about 20 years, they produce sporangia only very rarely under uniform watering conditions, in contrast to the situation in the field where whole stands may be fertile (T. G. Walker, pers. comm.).

Ceratopteris thalictroides (L.) Brongn., and *C. lockhartii* (Hook. & Grev.) Kunze may also be found in inner coastal swamps with *Marsilea* sp. and *Cyclosorus interrupta*.

Savanna

The term savanna is used to mean a short grass-sedge community with occasional shrubs, usually on firm white (leached) sands and not in swamps. Occasionally where hollows do form and give rise to marsh forest, the margin of such communities is characteristically ringed by so-called *palm marsh*, an association of *Bactris* sp., *Mauritia*, and *Chrysobalanus*, with *Blechnum serrulatum* mentioned above. Epiphytes on the palms include *Lycopodium linifolium, Nephrolepis rivularis* (Vahl) Mett., *Oleandra articulata, Polypodium brasiliense* Poiret, and *Trichomanes arbuscula* Desv.

The open savanna is dominated by sedges (*Rhynchospora holoschoenioides* (L. C. Rich.) Herter, *R. globosa* Roemer & Schultes, etc.) and with *Paspalum pulchellum* Hochst., *Lagenocarpus tremulus* Nees, *Xyris grisebachii* Malme, and the orchids *Epistephium parviflorum* Lindl., *Pogonia rosea* (Lindl.) Reichb. f., *Otostylis brachystalix* (Reichb. f.) Schltr., and

Cyrtopodium sp. (Richardson, 1963). *Lycopodiella caroliniana* (L.) Pichi-Serm. is found here in communities that are sporadically burnt. Kornas (1979) found similar resistance to fire in this species in Zambia.

A scrub of *Byrsonima-Chrysobalanus* is found where *Lindsaea portoricensis* Desv., *L. stricta* (Swartz) Dryander var. *parvula* (Fée) Kramer and, most characteristically, *Schizaea pennula* (Swartz) Hook. were common. Large plants of *Pityrogramma calomelanos* were seen here with fronds up to 200 cm and turning reddish before dying; they proved to be hybrids (Walker, 1985).

Man-made habitats

Fern species that can withstand open conditions can be incorrigible weeds, and any new road opened up in the clay soils of the tropics, especially when these cut into the side of a mountain and present steep clean-cut banks, will soon have a dense fern tangle. *Gleichenia* is dominant on such banks and *G. bifida* (Willd.) Sprengel, *G. interjecta* Jermy & T. Walker, and *G. remota* (Kaulf.) Sprengel are common right to the mountain tops, frequently with their hybrids; *Dicranopteris pectinata* L. Underw. is less abundant. Haufler & Adams (1982) draw attention to the three dimensional gametophyte of *G. bifida* and suggests it would confer an advantage to the species during the daily fluctuation in solar radiation, over a flat, plate-like prothallus which would lose more water. Stokey (1950) indicates that gametophytes of this species reach sexual maturity more rapidly than any other member of the Gleicheniaceae she had studied. This also would be beneficial in such exposed habitats.

The following species formed a typical species assemblage on the roadbanks of the Northern Range: *Adiantopsis radiata* (L.) Fée, *Adiantum obliquum, A. petiolatum* Desv., *A. terminatum* Kunze, *A. tetraphyllum, Anemia pastinacaria* Prantl, *A. phyllitidis* (L.) Swartz, *Blechnum occidentale, B. fraxineum, Cyathea microdonta, C. spectabilis, Hemionitis palmata* L., *Lindsaea portoricensis, Lycopodiella cernua, Nephrolepis biserrata* (Swartz) Schott, *N. exaltata* (L.) Schott, *Selaginella cladorrhizans, S. diffusa* (C. Presl) Spring, *S. mnioides* A.Braun, *S. platybasis* Baker, *S. trifurcata* Baker, and *Trichomanes pinnatum* Hedwig.

In wet runnels along roadsides *Cyclosorus interrupta* is frequent and *Trichomanes pinnatum* Hedwig is sometimes found, often in full sun. It may be noted (Walker, pers. comm.) that meiosis in filmy ferns virtually ceases in pronounced dry seasons, whereas in *Gleichenia*, for example, it continues throughout. In Britain, in cultivation, most tropical ferns have two major spore-producing flushes, spring and autumn, when day and nights are more or less equal as in the tropics.

The following points may be made on individual species. *Anemia pastinacaria* has a very marked seasonal growth pattern, and during the wet season the fronds were all green and producing spores abundantly. In the dry season T. G. Walker (pers. comm.) reports that plants from the same locality were in a state of dormancy with the fronds brown and crisp. In patches the bank had been burnt over and the *Anemia* plants survived this treatment. On sending the dormant rhizomes back to Newcastle, the dormancy was quickly broken by regular watering and new fronds were rapidly produced. This behaviour corresponds to that shown in the Type III 'summer green' pattern noted by Kornas (1977) for a number of ferns growing in the seasonal climate of Zambia. In this *Anemia* the dead fronds persist, attached to the rhizome for some time. The plants did not survive long enough in cultivation to observe if this seasonal pattern of events was genetically determined and would persist under a regular uniform regime of watering, as has been noted in *Adiantopsis radiata* (see below).

One of the prominent features of the genus *Adiantopsis* is the articulation of the pinnules to the stipicel, and, in the case of *A. radiata* at least, in the dry season the pinnules are frequently shed, leaving the black stipe and its branches bare. Eventually the stipe itself drops. This behaviour is evidently inherent, as, according to Walker (pers. comm.), in cultivation under a more or less uniform regime of watering, the plant continues to behave in the same way, losing first its pinnules and then its stipe. Normally there tends to be a short rest before the production of new fronds. It may be noted in passing that, unlike a number of ferns whose pinnules are deciduous, e.g. *Nephrolepis* spp., those of *A. radiata* do not shed when herbarium specimens are being prepared and thus behave like *Adiantum deltoideum* Swartz, in which herbarium plants show both bare stipes and fully furnished fronds as in nature.

Hemionitis palmata has accessory reproduction by bulbils borne on the fronds. Under damp conditions these bulbils grow and develop into new plants, whilst under dry conditions the buds remain inactive. When in a uniform environment of the greenhouse (Walker, pers. comm.) plants tend to die back irregularly, i.e. apparently not at any fixed period, although several plants in a pan tend to behave as a unit, all dying back together. The die-back does not appear to be related to dry conditions in the field, as the species in Jamaica tends to live in rather dry situations and is fertile at most times of the year.

In areas such as Trinidad dry-season fires are ecologically important. Kornas (1979) discusses this factor in detail for Zambia. He mentions no information being available for the fire resistance or susceptibility of *Pteris vittata* L. Walker records (pers. comm.) collecting a specimen on an open rocky grassed area near Port of Spain where fire had previously raged. Other species there included *Adiantum lucidum* (Cav.) Swartz and *A. villosum*. Similarly the only stand of *Pteridium aquilinum* var. *arachnoideum* (Kaulf.) Brade in Trinidad is subject to seasonal fires.

Cocoa plantations are shady and have a characteristic ground flora which includes several *Adiantum* species (e.g. *A. macrophyllum* Swartz, *A. tetraphyllum*), *Asplenium laetum* Swartz, *Goniopteris poiteana, Selaginella diffusa*, and on the trees themselves *Polypodium phyllitidis* and *Polytaenium brazilianum* (Desv.) Bened. *Ananthacorus angustifolius, Lycopodium* spp., *Lygodium micans* Sturm, and *L. venustum* Swartz are common at the edges of such plantations, in gardens, and along the borders of secondary scrub.

Acknowledgements

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Cytotaxonomic studies of the ferns of Trinidad

2. The cytology and taxonomic implications

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Synopsis

Several visits to Trinidad and Tobago provided material for the cytotaxonomic study on ferns which is described here. Cytological information is available for 155 taxa or cytotypes, and the notes on individual taxa amplify some of this information both in regard to taxonomic problems and to interrelationships on the specific or generic level. An important new development in technique is the production of standardised karyotypes of a number of taxa and some of the uses to which analyses of them may be put are discussed. Taxonomic implications resulting from these cytological studies are discussed and some morphological features of the taxa and hybrids concerned are compared.

The fern flora of Trinidad contrasts with that of Jamaica in having a significantly lower incidence of polyploidy and the possible reasons for this are discussed. However, similarities are shown with Jamaica in the commonplace occurrence of hybridity and the rarity of agamospory.

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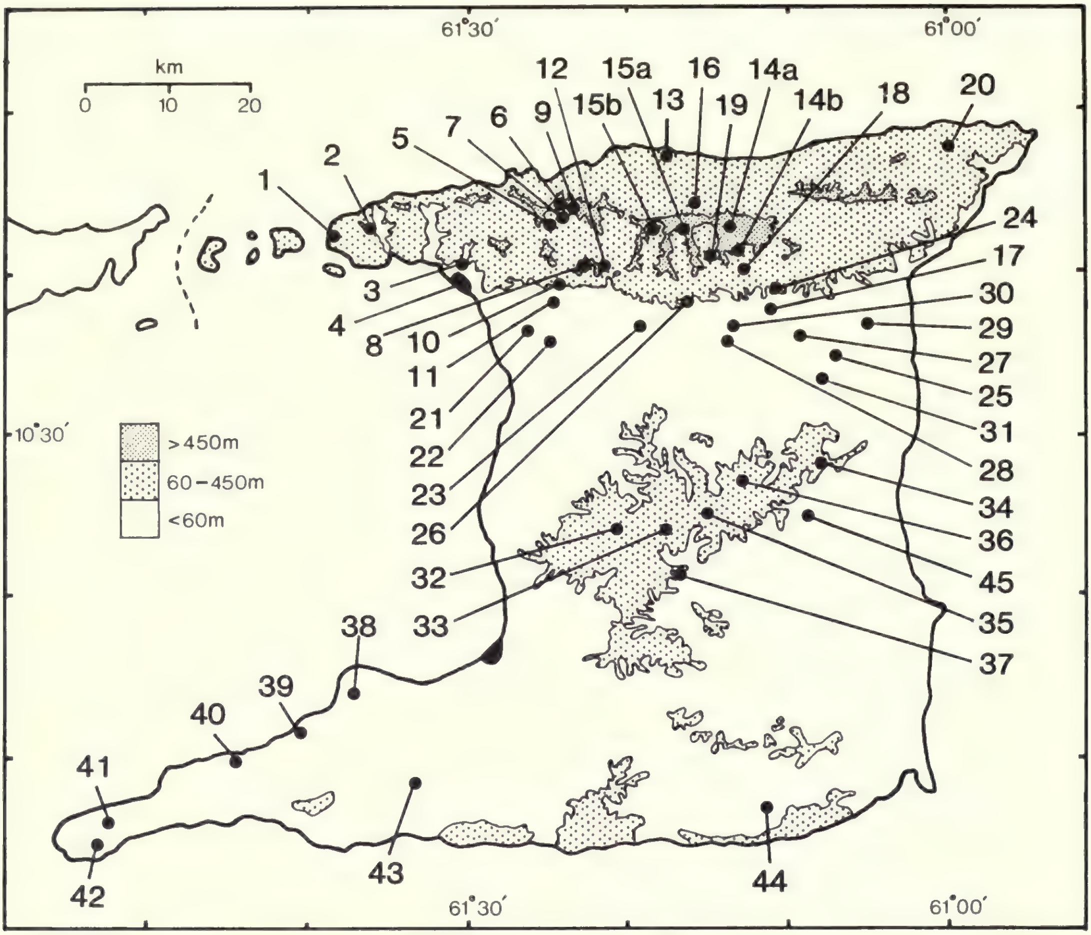
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Fig. 1 Map of Trinidad showing collecting localities.
1 Scotland Bay. 2 Morne Catherine. 3 Lady Chancellor Road, St Anns. 4 Port of Spain. 5 Loanga. 6 El Tucuche. 7 Maracas Falls. 8 Mt Tabor. 9 Naranja. 10 St John's Valley, Tunapuna. 11 St Augustine. 12 Caura Valley. 13 Blanchisseuse. 14a Aripo Heights. 14b Aripo Valley. 15a Morne Bleu – Blanchisseuse Road – La Laja. 15b Las Lapas Trace. 16 Brasso Seco. 17 Long Stretch Reserve. 18 Aripo Road. 19 Guanapo Valley. 20 Grand Fond Road. 21 Caroni Swamp. 22 Princess Margaret Highway. 23 Churchill-Roosevelt Highway. 24 Valencia. 25 Sangre Grande. 26 Arima. 27 Guiaco-Valencia Forest Reserve. 28 Arena Forest Reserve. 29 Melajo Forest Reserve. 30 Aripo Savanna. 31 Near Guiaco, confluence of rivers. 32 Corosal Hill. 33 Tabaquite. 34 Mt Harris. 35 Brasso Venado. 36 Mt Tamana. 37 Brickfield. 38 Pitch Lake. 39 Point Fortin Experimental Farm. 40 Irois. 41 Grass swamp near Fullarton. 42 Icacos Point swamp. 43 Quarry Forest. 44 Texaco Village, Trinity Hills. 45 Biche.

Introduction

Whilst carrying out a cytotaxonomic investigation of the fern flora of Jamaica (Walker, 1966*a*, 1973*b*), it was felt to be desirable that another part of the Caribbean region should be examined for comparative purposes and to test overall conclusions. Trinidad was considered to be ideal for such an investigation, being at the other end of the chain of West Indian islands from Jamaica and lying so close to the South American mainland that floristically it can be regarded as part of the latter. An account of the general environment of Trinidad is given in paper 1 of this trilogy (Jermy, 1985).

The present survey of the cytology of the fern flora of Trinidad and Tobago is the outcome of three major periods of field work carried out from 1963 to 1974, and the subsequent cultivation of plants at the University of Newcastle upon Tyne and the Royal Botanic Gardens, Kew. These were integrated with laboratory studies at Newcastle by T. G. Walker and herbarium studies at the British Museum (Natural History) by A. C. Jermy.

The first and most comprehensive collecting expedition was made in July to September 1963 by the author and A. C. Jermy with the financial support of the Nuffield Foundation, the Godman Exploration Fund, and of the respective institutions. A second visit in April 1966 by T. G. and M. G. Walker was also supported by the Nuffield Foundation. A further visit by A. C. Jermy, funded by the British Museum (Natural History) and accompanied by J. Simmons (R.B.G., Kew) in August to October 1974 allowed collecting to extend to Tobago. The locations of the collecting sites are shown in Fig. 1. One advantage of the visit occurring in April was that this was during the marked dry season and observations were made as to how some of the ferns reacted to this rainless period. In addition to the above, a small but very valuable amount of material has also been made available by other collectors, in particular Dr Alice Fay.

During the survey it became clear that five previously unrecognised taxa were present and these, together with nine of the 14 different hybrid combinations found, have been described and validated in paper 3 (Jermy & Walker, 1985). In addition a new combination has been made there, namely in *Meniscium*.

In the notes the arrangement and concept of families and genera follow those of Crabbe, Jermy & Mickel (1975), with the exception of *Polypodium* s.l. where the segregate genera are simply indicated informally.

Materials and methods

Chromosome fixing and karyotyping

Cytological fixations were made in the field in 1963 and 1966 and have been heavily supplemented by those made on the living collections at Newcastle and Kew. The methods involved in obtaining meiotic and root tip squashes are standard, whilst the supplementary use of young croziers as a source of dividing somatic cells in those epiphytes in which roots either developed only very sparsely or which cannot be cropped without great disturbance to the plant, have been described previously (Walker, 1973*b*). Voucher specimens of all cytologically authenticated material are deposited in BM, with duplicates, where available, in TRIN and herb. T. G. Walker.

Karyotyping has been carried out for a number of species. This has raised problems of how to show the essential facts in the most economical manner and in a form which can be standardised for comparative work in the future. Many attempts were made before evolving a method which appears to achieve these aims. One of the principal difficulties encountered in fern karyotypes as opposed to those of other organisms is a direct consequence of the numbers involved. Whilst different forms of chromosomes may be perfectly obvious in a plant with say $2n = 10$ (Fig. 2) the same forms may not be so immediately obvious when part of a chromosome complement of $2n = 74$ for example (Fig. 28B). Furthermore, there is no standard way of setting out the data and

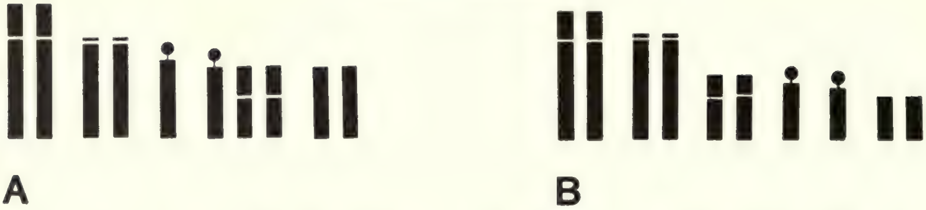

Fig. 2 Complements of 2n = 10 extracted from karyograms of: **A**, *Polypodium latum* (2n = 74). **B**, tetraploid *P. aureum* (2n = 148). Compare with the complete karyograms in Figs 29 and 25C respectively.

almost any issue of a journal in which a high proportion of its articles are devoted to karyotypic studies (e.g. *Cytologia*, 1978) will show a multiplicity of methods of presentation. Whilst it is true that a number of papers concerned with fern karyotypes have been published by Japanese workers, viz. Kawakami (1970, 1971), Takei (1969), Tatuno & Kawakami (1969), Tatuno & Okada (1970), Tatuno & Takei (1969*a* & *b*), Tatuno & Yoshida (1966, 1967), these have been undertaken predominantly with a particular end in view, namely the demonstration of alleged ancestral basic chromosome numbers (b). Their methods have not proved to be particularly suitable for the present purposes and hence an independent system has had to be devised.

It has been found in a much wider survey of fern karyotypes (Walker, unpub.) that a study of chromosome length can give very useful information. In order to get the most informative results experiments were carried out to determine the most satisfactory means of measurement that would be both accurate and at the same time produce suitable groupings or classes of chromosome length which could be illustrated graphically and from which valid inferences could be made. The method adopted here appears to meet these criteria and involves photographing well-spread somatic metaphase nuclei and enlarging to a magnification of × 3000. The individual chromosomes are measured on the enlargements to the nearest mm, each 1 mm representing a 'unit of length'. Such a unit is equal to 0·33 μm actual length. Thus a chromosome of say 19 units length is actually 6·33 μm long. However, for most purposes it is more convenient to use the units of length as they stand rather than to convert them. This method of measurement has proved to give a very satisfactory grouping of results. If the measurement is made to an allegedly greater degree of accuracy, the accuracy becomes more apparent than real – see Bentzer et al. (1971) whilst if smaller units of length are employed the overall pattern tends to be obscured. Conversely, if these units are larger this produces too little separation of the length classes in those species which show only a very small range in actual lengths of the chromosomes such as in diploid *Polypodium aureum* (from 2·0 μm to 4·0 μm). Thus measurements taken from enlargements of × 4000 and × 2000 fail to meet the requirements set out above.

The karyograms are stylised whereby the chromosomes are presented as solid columns of uniform width in which the length and centromere positions, together with satellites if present, are depicted accurately in standard form. All chromosomes of the same length are grouped together, starting in each group with those in which the centromere is most nearly median and finishing with those in which it is most nearly terminal. The length of the chromosomes is given below each group in units of length and, as has been noted above, these may be converted to actual measurements by dividing this figure by 3·0.

The total number of chromosomes in a complement with their centromere positions is presented in the form of Tables, the nomenclature used being that of Levan, Fredya & Sandberg (1965). In their system two fixed *points* of a chromosome are recognised, the median point (M) which is at the exact mid-point of the chromosome and the terminal point (T) at the extreme end. The chromosome arm between these two points is divided into four equal *regions* these being, from the centre to the end, the median region (m), the submedian region (sm), the subterminal region (st) and the terminal region (t). Levan et al. (1965) gives several methods of calculating the centromere position, the one used here involving the ratio of the length of the long arm to the

Table 1 L/S ratios and centromere positions.

Centromere position	Ratio as in Levan et al. (1965)	Ratio used in present survey
Median point (M)	1·0	1·0
Median region (m)	1·0–1·7	>1·0–1·7
Submedian region (sm)	1·7–3·0	>1·7–3·0
Subterminal region (st)	3·0–7·0	>3·0–7·0
Terminal region (t)	7·0–∞	>7·0–<∞
Terminal point (T)	∞	∞

length of the short arm of the chromosome, L/S. In the original paper the values for the ratios overlap at one or both end-points in each centromere range and this can lead to ambiguity e.g. a chromosome with a ratio of 3·0 could be classed as having its centromere either in the submedian or in the subterminal region (see Table 1). To obviate such ambiguities I have as standard practice eliminated the points of overlap, thus a particular ratio value corresponds to only one centromere position.

Attention should be drawn to the fact that the T position is the least satisfactory one, all the others being easily determined. Here the centromere is deemed to be at the terminal point when no staining piece of chromosome can be detected distal to it. Such centromeres are very common in fern karyotypes but probably the T value quoted is an inflated one as it has been observed (Walker, unpub.) that a centromere may appear to be in the T position when the chromosomes are very contracted but may in fact be seen to be truly in the subterminal region (t) when the chromosomes are more relaxed. It is more probably the sum of the T + t centromeres that is important rather than both separately, although I have continued to record them as two categories.

In general, partly because of the large numbers of chromosomes involved and partly because even both members of an homologous pair do not always contract to exactly the same length it is not possible to say with certainty which chromosome is homologous to which other one, only to establish degrees of affinity, except in certain well-defined cases, e.g. those with median point centromeres, satellites, etc. However, this lack of absolute precision does not affect the overall results and conclusions.

For several species, in addition to the karyograms and Tables of centromere positions, the chromosome lengths have been presented in the form of histograms to illustrate specific points, and in particular to show deviations from the normal distribution curve which is typical of so many species. In a few cases conclusions drawn from the karyotypic data are stated without entering into detailed explanations as to how these conclusions have been reached. Such conclusions are based on more extensive work on ferns from other parts of the world and will be reported on in detail elsewhere.

Karyotyping of ferns is still in its infancy and whilst it has been possible in a number of instances to draw conclusions it is equally important to collect as much data as possible which may be used to make comparisons and from which general principles may be extrapolated in the future. It is to these ends that the information is given here in what it is hoped may become a standard system of presentation, or at least one that can be adapted with a minimum of effort.

Spore and stomata measurements

Spore lengths are quoted in a number of cases and these are based on samples of 50 individual measurements made on specimens mounted in Euparal. The length is taken to include the perispore wing when present and the means, minima and maxima quoted have been rounded to the nearest 0·5 μm. The same sample sizes and approximations apply also to any stomatal lengths that are quoted. Stomatal lengths were measured on reconstituted, stained herbarium material, prepared as follows. Conveniently sized pieces of lamina were placed in a 6% aqueous potassium hydroxide solution to which an equal quantity of decolourised Fuelgen reagent was added and the whole incubated in an oven or on a hot-plate at *c.* 60°C overnight. After draining off the reagent and rinsing two or three times in water the material was taken up to 50% alcohol for examination and measurement. This treatment fully re-expands the cells and provides sufficiently intense magenta staining for accurate measurement.

Notes on individual taxa

Table 2 summarises the cytological results of this survey and gives the names of the authors of the taxa discussed. Both there and in the following text the term agamospory or agamosporous has been used in opposition to the term sexual. This replaces the inaccurate but very widely used terms apogamous or apogamy. For readers unfamiliar with the details of the several patterns of sporogenesis included under these terms comparative accounts are to be found in Lovis (1977) and Walker (1966*b* & 1979).

Table 2 List of taxa and chromosome numbers. Collection numbers prefixed with J are collections of A. C. Jermy, those with T are of T. G. Walker. Locality numbers refer to map in Fig. 1. I and II indicate univalents and bivalents respectively. In Hymenophyllaceae the ploidies are given in parentheses to indicate the comparative levels attained as the original base numbers are debatable (see p. 179).

Taxon	Voucher collection No.	Locality reference	Chromosome number	Ploidy
FAM. I. MARATTIACEAE				
Danaea elliptica Smith	T6715, T7066	14b	$n = 80$	4x
D. nodosa (L.) Smith	T6580	33	$n = c.\ 80$	4x
FAM. II. SCHIZAEACEAE				
Schizaea pennula (Swartz) Hook.	T6294, T6301 T6307, T6327 T7374, T7378 T7380, T7388	30	$n = 134$	?
Lygodium venustum Swartz	J10844:1	12	$2n = 116$	4x
L. micans Sturm	J11001	8	$2n = 58$	2x
Anemia pastinacaria Prantl	T6027, T6028 T6036, T6038 T6040, T6041 T6043, T6044	12	'n' = 114 IIs and 38 Is + 38 IIs	3x agamosporous
A. phyllitidis (L.) Swartz	Fay 417	8	$n = c.\ 76$; $2n = c.\ 152$	4x sexual
FAM. III. ADIANTACEAE: ADIANTOIDEAE				
Adiantopsis radiata (L.) Fée	J2045	12	$2n = 60$	2x
	J10999:3	10	$2n = 60$	2x
Pityrogramma calomelanos (L.) Link	T6354	30	*c.* 76 Is + *c.* 37 IIs, meiosis irregular	5x sterile hybrid
Hemionitis palmata L.	T6088	12	$n = 30$	2x
Adiantum latifolium Lam.	T6444	15a	$n = 60$; $2n = 120$	4x
A. lucidum (Cav.) Swartz	T11066, T11072	3	$n = 30$; $2n = 60$	2x
	T7397, T11067 T11068, T11071	3	$2n = 60$	2x
	J10996, J10978:3	10	$2n = 60$	2x
A. macrophyllum Swartz	T6667	18	$n = 30$	2x
	J11047	16	$n = 30$	2x
A. petiolatum Desv.	T6064	12	$n = 30$	2x
	T10523	12	$2n = 60$	2x
	J10945	16	$n = c.\ 30$	2x
	J11332	Tobago	$2n = 60$	2x
A. pulverulentum L.	T10632	7	$n = c.\ 30$	2x
	T10633	7	$2n = 60$	2x
	T10634	7	$n = c.\ 30$; $2n = 60$	2x
	T6614	37	$n = 122$	hyper-8x

Table 2 – *cont.*

Taxon	Voucher collection No.	Locality reference	Chromosome number	Ploidy
A. terminatum Kunze	T6111	12	n = 60	4x
	T6435	15a	n = 60	4x
A. tetraphyllum Humb. & Bonpl. ex Willd.	T10548	12	2n = 62	2x aneuploid
	J10874:1	15b	2n = *c.* 60 Bidin (1980)	
			2n = 58	2x
	J10874:2	15b	2n = *c.* 60	2x
	J10930:1	29	2n = *c.* 120	
			2n = 117 Bidin (1980)	4x aneuploid
	J10930:2	29	n = 60	4x
	J11065:1	2	2n = *c.* 120;	
			2n = 114 Bidin (1980)	4x aneuploid
	J11279	Tobago	2n = *c.* 120;	
			n = 58 Bidin (1980)	4x
	Simmons 171	13	2n = 58 Bidin (1980)	2x
A. × *variopinnatum* Jermy & T. Walker	J11061	2	90 chromosomes, meiosis irregular	3x sterile hybrid
(= *A. latifolium* × *petiolatum*)	J10993	10	90 chromosomes, meiosis irregular	3x sterile hybrid
	T6122, T6123	12	90 chromosomes, meiosis irregular	3x sterile hybrid
A. villosum L.	T11085	3	2n = 60	2x
	T11082	3	n = 30; 2n = 60	2x sexual
A. × *villosolucidum* Jermy & T. Walker	T10588, T10589	12	2n = 60; meiosis irregular	2x sterile hybrid
(= *A. lucidum* × *villosum*)	T10590, T10591 T10592	12	2n = 60	2x sterile hybrid
FAM. III. ADIANTACEAE: VITTARIOIDEAE				
Polytaenium cajenense (Desv.) Benedict	T7269	19	n = 60	4x
P. feei (Schaffner ex Fée) Maxon	J11260	14a	2n = 120	4x
Anetium citrifolium (L.) Splitg.	T7037	14a	n = 60	4x
FAM. III. ADIANTACEAE: PTERIDIOIDEAE				
Pteris arborea L.	T7084	14a	n = 58	4x
P. inaequalis (Fée) Jenman	T6220	7	n = 58	4x
	T6792	6	n = 58	4x
	T10652, T10660 T10763, T10765	7	2n = 116	4x
	J11235	6	2n = *c.* 116	4x
	J11010:3	44	2n = *c.* 116	4x
P. longifolia L.	T11061	3	n = 58	4x
	T11062	3	n = 58; 2n = 116	4x
	J11064:2	2	n = *c.* 58	4x
P. tripartita Swartz	T6167, T6168	33	n = 58	4x
	T7060	17	n = 58	4x
	T11026	7	2n = *c.* 116	4x
Acrostichum danaeifolium Langsd. & Fischer	T6935	42	n = *c.* 30; 2n = *c.* 60	2x
	T10917	30	2n = 60	2x

Table 2 – *cont.*

Taxon	Voucher collection No.	Locality reference	Chromosome number	Ploidy
FAM. IV. HYMENOPHYLLACEAE				
Mecodium polyanthos (Swartz) Copel.	T6825, T6920	6	n = 28	(2x)
	T7273	19	n = 28	(2x)
Sphaerocionium hirsutum (L.) C. Presl	T6828, T6829	6	n = 36	(2x)
	T7317	7	n = 36	(2x)
S. × *tucuchense* Jermy & T. Walker (= *S. ?elegans* Sprengel × *hirsutum*)	T6898	6	72 chromosomes, meiosis irregular	(2x) sterile hybrid
	T6571	15a		
Vandenboschia hymenophylloides (Bosch) Copel.	T7036	14a	n = 36	(2x)
	T11012	6	n = 36	(2x)
Trichomanes arbuscula Desv.	T6383, T6386 T6393, T6396	30	n = 64	(4x)
T. crispum L.	T6899	6	n = 128	(8x)
T. crispum × *?robustum* s.l.	T6821	6	192 chromosomes; meiosis irregular	(6x) sterile hybrid
T. fimbriatum Backhouse ex T. Moore	T6830	6	n = *c.* 64	(4x)
T. pinnatum Hedw.	T7062, T7064	12	n = 32	(2x)
Feea osmundoides s.l. hybrid	T6555, T6556 T6557, T6565	15b	64 chromosomes; meiosis irregular	(2x) sterile hybrid
Selenodesmium rigidum (Swartz) Copel.	T7194	15a	n = 33	(2x)
Davalliopsis elegans (L. C. Rich.) Copel.	T6698, T6704 T6707	14b	n = 32	(2x)
Didymoglossum angustifrons Fée	T7040	14a	n = 34	(2x)
Microgonium kapplerianum (Sturm) Pichi-Serm.	T7038	14a	n = *c.* 68	(4x)
Lecanolepis membranacea (C. Presl) Pichi-Serm.	T7032, T7266	19	n = 34	(2x)
	Jermy s.n.	16	n = 34	(2x)
FAM. V. GLEICHENIACEAE				
Dicranopteris pectinata (Willd.) L. Underw.	T6083	12	n = 43	2x
	T6420	15a	n = 43	2x
	T7321	7	n = 43	2x
	T10300, T10301 T10303	14b	n = 43	2x
	T10802, T10803 T10804	15a	n = 43	2x
Gleichenia bifida (Willd.) Sprengel	T10331	14b	n = 34	2x
	T10800	15a	n = 34	2x
G. interjecta Jermy & T. Walker	T10332	14b	n = 68	4x
G. remota (Kaulf.) Sprengel	T10335	14b	n = 34	2x
G. × *pseudobifida* Jermy & T. Walker (= *G. bifida* × *interjecta*)	T10324, T10327 T10328, T10329 T10330, T10333	14b	34 Is + 34 IIs; meiosis irregular	3x sterile hybrid
	T6414, T6415 T6417	15a	34 Is + 34 IIs; meiosis irregular	3x sterile hybrid
	T10801, T10805 T10806, T10807 T10808, T10810 T10811	15a	34 Is + 34 IIs; meiosis irregular	3x sterile hybrid
G. × *subremota* Jermy & T. Walker (= *G. interjecta* × *remota*)	T6416	15a	34 Is + 34 IIs; meiosis irregular	3x sterile hybrid
G. brittonii (Maxon) C.Chr.	T6789	6	n = 34	2x

Table 2 – *cont.*

Taxon	Voucher collection No.	Locality reference	Chromosome number	Ploidy
FAM. VI. POLYPODIACEAE: PLEOPELTOIDEAE				
*Dicranoglossum desvauxii** (Klotzsch) Proctor	T7076	14a	n = *c.* 72	4x
FAM. VI. POLYPODIACEAE: POLYPODIOIDEAE				
Polypodium loriceum L. (= subg. *Polypodium*)	T6809	6	n = 37	2x
P. sororium Humb. & Bonpl. ex Willd. (= subg. *Polypodium*)	T6233	7	n = 74	4x
	T6925	15a	n = 74	4x
P. triseriale Swartz (= subg. *Polypodium*)	T6486, T6547	15a	n = 37	2x
	T6344	30	n = 37	2x
	T6349	30	n = 37; 2n = 74	2x
P. ptilodon var. *pilosum* A. M. Evans (= subg. *Polypodium*)	T7262	19	n = 37; 2n = 74	4x
P. polypodioides (L.) Watt (= subg. *Polypodium*)	Trinidad sine coll. et no.	45	n = 74	4x
P. aureum L. (= subg. *Phlebodium*)	T6628	37	n = 74	4x
	J11325:1	Tobago	2n = 148	4x
	J11325:2	Tobago	2n = 148	4x
P. decumanum Willd. (= subg. *Phlebodium*)	T6990, J2817	39	2n = 74	2x
	T7212	7	2n = 74	2x
P. latum (T. Moore) T. Moore ex Sodiro (= subg. *Campyloneurum*)	T10605	7	n = 37; 2n = 74	2x
	J11044:1	16	n = 37; 2n = 74	2x
	J11214	16	n = 37	2x
	J11041:1, J11057	16	2n = 74	2x
	J10986	8	2n = 74	2x
P. phyllitidis L. (= subg. *Campyloneurum*)	T7253, T7256	20	n = 74	4x
	T7255	20	n = 74; 2n = 148	4x
	T11060	3	2n = *c.* 148	4x
	J10994:1	10	2n = 148	4x
	J10986:3, J10984	8	n = 74	4x
	J10986:2	8	2n = *c.* 148	4x
	J10986:1	8	n = 74; 2n = 148	4x
	J11326, J11366	Tobago	2n = *c.* 148	4x
P. ciliatum Willd. (= subg. *Microgramma*)	T6199	33	n = 37	2x
P. lycopodioides L. (= subg. *Microgramma*)	T10883	15a	n = 37	2x
FAM. VII. GRAMMITIDACEAE				
Grammitis taenifolia (Jenman) Proctor	T6811	6	2n = 74	2x
Cochlidium linearifolia (Desv.) Maxon	T6810	6	n = *c.* 36	2x
Xiphopteris serrulata (Swartz) Kaulf.	T10976	6	'n' = 105 Is	3x agamosporous
	Trousdell 77	6	'n' = 105 Is	3x agamosporous
FAM. VIII. CYATHEACEAE				
Cyathea aspera (L.) Swartz (= *Trichipteris*)	T6412	15a	n = 69	2x
C. microdonta (Desv.) Domin (= *Trichipteris*)	T7018	19	n = 69	2x
	J10984	15a	n = 69	2x
C. sagittifolia (Hook.) Domin (= *Trichipteris*)	T6831	6	n = 69	2x
	Trousdell 69	6	2n = *c.* 138	2x

* A specimen collected in Brazil (hort. Kew) proved to be n = 36 (2x).

Table 2 – *cont.*

Taxon	Voucher collection No.	Locality reference	Chromosome number	Ploidy
C. surinamensis (Miq.) Domin (= *Sphaeropteris*)	T6487	15a	n = 69	2x
	T6713	14b	n = 69	2x
C. spectabilis (Kunze) Domin (= *Cnemidaria*)	T6068	12	n = 69	2x
	T6991, T6992	15a	n = 69	2x
C. tenera (Hook.) T. Moore (= *Cyathea*)	T7082	14a	n = 69	2x
FAM. IX. DENNSTAEDTIACEAE: DENNSTAEDTIOIDEAE				
Dennstaedtia bipinnata (Desv.) Maxon	J11141	6	n = *c.* 94	4x
	J11155	14b	2n = *c.* 188	4x
D. obtusifolia (Willd.) T. Moore	T10600	7	n = 46	2x
	T10795	15a	n = 46	2x
Pteridium aquilinum var. *arachnoideum* (Kaulf.) Brade	T11056	3	2n = 104	4x
FAM. IX DENNSTAEDTIACEAE: LINDSAEOIDEAE				
Lindsaea lancea var. *falcata* (Dryander) Rosenst.	T10779	17	n = 41–44	2x
L. portoricensis Desv.	T6647	17	n = *c.* 88	4x
	T10355	14b	n = 86–88	4x
L. stricta (Swartz) Dryander var. *stricta*	T6070	12	n = *c.* 88	4x
L. stricta var. *parvula* (Fée) Kramer	T6357, T6368	30	n = *c.* 88	4x
FAM. X. THELYPTERIDACEAE				
Amauropelta oligocarpa (Humb. & Bonpl. ex Willd.) Pichi-Serm.	T10674, T10688	6	n = 29	2x
A. opposita (Vahl) Pichi-Serm.	J11071	15a	2n = 58	2x
	J11296	Tobago	2n = 58	2x
Macrothelypteris torresiana (Gaud.) Ching	T6258, J2235	7	2n = 124	4x
Goniopteris paucijuga (Klotzsch) Pichi-Serm.	T7056	14a	2n = 72	2x
G. pennata (Poiret) Pichi-Serm.	T10555, T10557	12	n = 36	2x
G. poiteana (Bory) Ching	T6138	12	n = 72	4x
	T10891	7	n = *c.* 72	4x
	J11331	Tobago	n = *c.* 72, 2n = *c.* 144	4x
G. nephrodioides (Klotzsch) Proctor	T6796	6	n = 72	4x
G. × *tabaquitensis* Jermy & T. Walker (= *G. paucijuga* × *tetragona*)	T6191, T6193 T6194	33	108 chromosomes; meiosis irregular	3x sterile hybrid
G. tetragona (Swartz) C. Presl	T7206	32	n = 72	4x
	J11336	Tobago	2n = *c.* 144	
Meniscium nesioticum (Maxon & C. Morton) Jermy & T. Walker	T7013, T7014 T7016	19	n = 72	4x
	T10479, T10480	12	n = 72	4x
M. serratum Cav.	T6160	33	n = 36	2x
	T6267, T6268 T6269, T6270 T6272, T6273	23	n = 36	2x
	J10930	29	2n = *c.* 72	2x
Christella dentata (Forssk.) Brownsey & Jermy	T11029	7	n = 72	4x
	J10943	16	2n = *c.* 144	4x
C. hispidulum (Decne) Holttum	T6184	33	n = 36	2x
	T10548	12	n = 36	2x
	J11095	15a	2n = 72	2x

Table 2 – *cont.*

Taxon	Voucher collection No.	Locality reference	Chromosome number	Ploidy
C. patens (Swartz) Holttum var. *patens*	T6781, T6782	18	$n = 36$	2x
	T10311	18	$2n = 72$	2x
	J11078, J11101 J11108:1	15a	$2n = 72$	2x
Amphineuron opulentum (Kaulf.) Holttum	T10312, T10340	18	$n = 72$	4x
	J10920	24	$n = 72$	4x
FAM. XI. ASPLENIACEAE: ASPLENIOIDEAE				
Asplenium abcissum Willd.	T6845	6	$n = 36$	2x
A. cristatum Lam.	J2382, J11258:10	14a	$2n = c.\ 144$	4x
A. hostmannii s.l.	T6617	37	$n = 72$; $2n = 144$	4x
	J11370	Tobago	$2n = 108$, meiosis irregular, *c.* 36 Is + 36 IIs	3x sterile hybrid
	T7102	14a	*c.* 144 chromosomes; meiosis irregular	4x sterile hybrid
A. juglandifolium Lam.	T7044, T7046	14a	$n = 144$	8x
A. macilentum Kunze ex Klotzsch	T6833	6	‘n’ = 288 Is, $2n = 288$	8x agamosporous
A. salicifolium L.	T6595, T6596 T6599	33	$n = 144$	8x
A. serra Langsd. & Fischer	J3004	14a	$2n = c.\ 288$	8x
A. serratum L.	T6164	33	$2n = c.\ 288$	8x
A. subhastatum Hook.	T6806	6	$n = c.\ 144$	8x
FAM. XI. ASPLENIACEAE: ATHYRIOIDEAE				
Diplazium caracasanum (Willd.) Kunze	J10962:2	6	$2n = 82$	2x
	J11198	16	$2n = 82$	2x
D. × *papyraceum* Jermy & T. Walker	T6176, T6179 T6180	37	123 Is; meiosis irregular	3x sterile hybrid
D. aff. *centripetale* (Baker) Maxon	T7182	14a	$n = c.\ 82$	4x
D. cristatum (Desv.) Alston	T6121	7	$n = c.\ 82$	4x
	T10500	12	$2n = c.\ 164$	4x
D. grandifolium (Swartz) Swartz	T6608, T6609	33	$n = c.\ 164$	8x
D. aff. *striatum* (L.) C. Presl	T6216	7	$n = 164$	8x
Hemidictyum marginatum (L.) C. Presl	T6409, T6410 T10792	15a	$n = 31$	2x
	J10933:1, J11161	15a	$2n = 62$	2x
	J11194	15b	$n = 31$; $2n = 62$	2x
FAM. XI. ASPLENIACEAE: TECTARIOIDEAE				
Ctenitis aripensis (C.Chr. & Maxon) Lellinger	T7041	14a	$n = 41$	2x
C. kallooi Jermy & T. Walker	T6794	6	$n = 41$	2x
C. protensa var. *funesta* (Kunze) Proctor	T7252	27	$n = c.\ 82$	4x
C. sloanei (Poeppig ex Sprengel) Morton	T6676	14b	$n = 82$	4x
Lastreopsis effusa subsp. *divergens* (Willd. ex Schkuhr) Tindale	T10613	7	$n = 82$	4x
	T10573	12	$2n = c.\ 164$	4x
	T10568, T10569	12	$n = 82$; $2n = 164$	4x
Tectaria × *bulbifera* Jermy & T. Walker (= *T. incisa* × *vivipara*)	T6175	33	120 chromosomes; meiosis irregular	3x sterile hybrid
T. heracleifolia (Willd.) L. Underw.	J10989	8	$2n = c.\ 160$	4x

Table 2 – *cont.*

Taxon	Voucher collection No.	Locality reference	Chromosome number	Ploidy
T. incisa Cav.	T6136	12	2n = 160	4x
	T6148	12	n = *c.* 80	4x
	T6972	36	n = 80	4x
	J10971:1, J10971:2	15a	2n = *c.* 160	4x
	J10976:3	8	2n = *c.* 160	4x
	J11368	Tobago	n = 80	4x
T. plantaginea Maxon	T6691, T6695 T6696, T6731	14b	n = 40	2x
T. orbicularis Jermy & T. Walker	J10941:1	16	2n = *c.* 80	2x
T. ramkissoonii Jermy & T. Walker	T7088	14a	n = 80	4x
T. trifoliata (L.) Cav.	T6748	14b	n = 40	2x
T. vivipara Jermy & T. Walker	T6171, T6173	33	n = 40	2x
Hypoderris brownii J.Smith	J10970	15a	n = *c.* 40	2x
	T6205	7	n = 40; 2n = 80	2x
Cyclopeltis semicordata (Swartz) J.Smith	T7202, T7203	32	n = 41	2x
Didymochlaena truncatula (Swartz) J.Smith	T6456	14a	2n = *c.* 82	2x
FAM. XI. ASPLENIACEAE: DRYOPTERIDOIDEAE				
Polybotrya caudata Kunze	T6996	15a	n = *c.* 41	2x
	J11158	15a	n = 41	2x
	J10826	24	n = 41	2x
P. cervina (L.) Kaulf.	T6215	7	n = 41	2x
	T6998	15a	n = 41	2x
	T7261	19	n = 41	2x
	J10857	15b	n = 41	2x
	J10958 J10966:1, J10966:2	15a	2n = 82	2x
P. osmundacea Humb. & Bonpl. ex Willd.	J10924:1	27	2n = *c.* 82	2x
FAM. XI. ASPLENIACEAE: LOMARIOPSIDOIDEAE				
Bolbitis hemiotis (Maxon) Ching	J11156	14b	n = 41; 2n = 82	2x
	T10317	14b	2n = *c.* 164	4x
B. portoricensis (Sprengel) Hennipman	T7221	7	2n = *c.* 82	2x
Lomariopsis marginata Kuhn	T6214	7	n = 41	2x
	T6161	37	n = 41	2x
FAM. XI. ASPLENIACEAE: ELAPHOGLOSSOIDEAE				
Elaphoglossum crinitum (L.) Christ	T10989, T10990	6	2n = 82	2x
E. glabellum J.Smith	T7316	6	2n = *c.* 82	2x
E. herminieri (Borg & Fée) T. Moore	T7340	7	n = 41	2x
E. lingua (Raddi) Brackenr.	J2692	6	2n = 82	2x
E. longifolium (Jacq.) J.Smith	T7030	19	2n = *c.* 82	2x
	T7085	14a	n = 41	2x
	J11123:5	6	n = *c.* 41	2x
E. pteropus C.Chr.	T6895	6	2n = *c.* 82	2x
E. rigidum (Aublet) Urban	J11192:3	15b	n = 41	2x
E. schomburgkii (Fée) T. Moore	J11183:1	15a	2n = *c.* 82	2x
FAM. XI. ASPLENIACEAE: OLEANDROIDEAE				
Oleandra articulata (Swartz) C. Presl	T6405	30	n = 41	2x

Table 2 – *cont.*

Taxon	Voucher collection No.	Locality reference	Chromosome number	Ploidy
Nephrolepis biserrata (Swartz) Schott	T6987	39	n = 41	2x
N. rivularis (Vahl) Mett.	T6353	30	n = 41	2x
FAM. XII. BLECHNACEAE				
Blechnum ×*caudatum* Cav. (= *B. fraxineum* × *occidentale*)	T7226, T7232 T7260, T10717	7	93 chromosomes; meiosis irregular	3x sterile hybrid
	T10915	7	2n = 93; meiosis irregular	3x sterile hybrid
B. fraxineum Willd.	T6243	7	n = 31	2x
	J10981	8	2n = 62	2x
	Fay s.n.	s.loc.	2n = 62	2x
	T7230	7	n = 62	4x
	Fay NY3, Fay NY6	s.loc.	n = 62, 2n = 164	4x
B. occidentale L.	T6137, J10837	12	n = 62	4x
	T7241, T7243 T10908	7	n = 62	4x
	J10880, J10881:4 J10891:8	15a	2n = 124	4x
	J11278	Tobago	n = 62	4x
	J11282, J11283	Tobago	2n = 124	4x
B. serrulatum L. C. Rich.	T6937	42	n = 36	2x
(*B. indicum* sensu T. Walker, 1966*a*)	J11215:1, J11215:3	30	2n = 72	2x
Salpichlaena volubilis (Kaulf.) J.Smith	T6413	15b	n = 40	2x
	T10831	15a	n = 40	2x
	J10915	15a	2n = 80	2x
	J11293	Tobago	2n = 80	2x

I. MARATTIACEAE

1. **Danaea** Smith

Walker (1966*a*, 1973*b*) reported on the cytology of three species of this genus, namely *D. jenmanii* L. Underw. from Jamaica, *D. elliptica* from Trinidad and *D. simplicifolia* Rudge from Surinam. Each had a chromosome count of n = 80 or 2n = 160, which were assumed to be at the tetraploid level on a base number of x = 40 which is common to the five genera which have been examined in the family, results lacking only for *Archangiopteris* and *Protomarattia*. Although x = 39 has been found in some species of *Marattia* other members of the genus show x = 40 and the former number is considered to be secondarily derived. That the base number is indeed 40 in *Danaea* and not, for example, 20 is further supported by the finding in Jamaica (Walker, 1966*a*) of a triploid hybrid between *D. jenmanii* and *D. jamaicensis* L. Underw. which shows 40 bivalents and 40 univalents at meiosis.

The count of n = 80 for a Trinidadian plant of the small species *D. elliptica* was photographically validated (Walker, 1966*a*) and the same result has now been obtained from a second plant from the Aripo Valley. The much larger species, *D. nodosa*, with fronds up to 2 m long has also proved to be tetraploid with n = 80. Sorsa (in Odum & Pigeon, 1970) has recorded n = 116 for this species in Puerto Rico but this count is clearly discordant with present evidence and needs further investigation.

Because of the very characteristic morphology and the distribution restricted to the neotropics, *Danaea* has been separated off by some authors as a family *Danaeaceae*. However, the cytology does not warrant a split and details of the karyotype (Walker in prep.) indicates the affinity of *Danaea* to other members of *Marattiaceae*.

II. SCHIZAEACEAE

1. Schizaea Smith

Schizaea pennula grows locally in relative abundance on the raised banks well above the wet-season water level of Aripo Savanna. Despite the shortly creeping character of the rhizomes the fronds are very tightly tufted. Digitate fertile regions or sorophores seen on the fronds of this species characterise a small group having a wide world-distribution and which some authors, e.g. Lellinger (1969), Bierhorst (1971) and Pichi Sermolli (1977), maintain as a distinct genus *Actinostachys*, in contrast to members of *Schizaea* s.str. which have pinnate sorophores. Cytologically the two genera or subgenera, if they be recognised as such, are very similar in having high chromosome numbers and *S. pennula* is no exception, with n = 134 being very clearly demonstrated in two specimens (Fig. 3) and approximately confirmed in another six plants. A very wide range of chromosome numbers, up to n = *c.* 540, has been demonstrated for the dozen or so species which have been examined and these are set out in Table 3.

Other unpublished counts by myself on several plants from Papua New Guinea and Sarawak confirm the general picture with gametic numbers ranging from n = *c.* 76 to n = *c.* 100. It is evident that in *Schizaea* there is a somewhat parallel situation to that found in *Ophioglossum* in which high chromosome numbers are involved and which undoubtedly represent high levels of polyploidy coupled with loss or gain of individual or small numbers of chromosomes. No doubt individual genes are present in multiplicate so that loss or gain of a few chromosomes has little effect on the viability or fertility of the plant, thus permitting the accumulation of a series of numbers which make little or no arithmetical sense. What is certain is that the assertion that these chromosome numbers probably derive from base numbers of 9, 11, and 12 (Pichi Sermolli, 1977) cannot be maintained on present evidence.

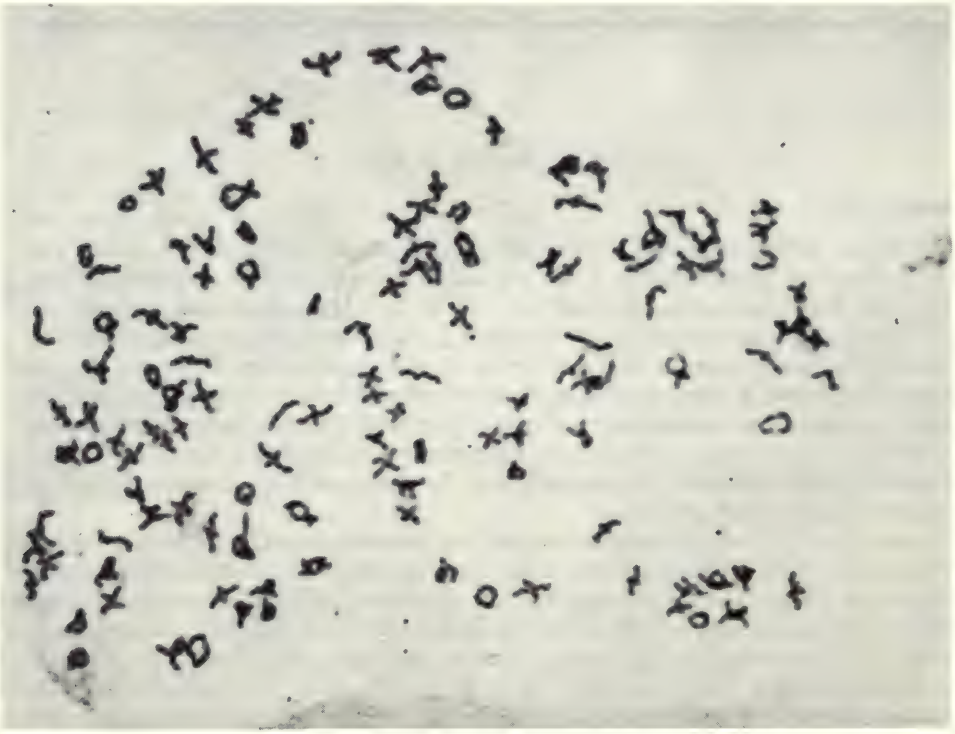

Fig. 3 *Schizaea pennula,* T7378, meiosis showing 134 bivalents, × 1000.

Table 3 Chromosome numbers in *Schizaea* s.lat.

Species	Chromosome number	Locality	Author
Subgenus *SCHIZAEA*			
S. fluminensis Miers ex Sturm	n = *c.* 72	Brazil	Araujo (1976)
S. asperula Wakef.	n = 77	New Zealand	Lovis (1958)
S. dichotoma (L.) Smith	n = 77	New Zealand	Lovis (in Holttum, 1959)
S. fistulosa Labill. var. *australis* (Gaudich.) J. D. Hook.	n = 94	New Zealand	Brownlie (1965)
S. robusta Baker	n = 96	Hawaii	Wagner (1963)
S. pulsilla Pursh	n = 103	U.S.A.	Wagner (1963)
S. incurvata Schkuhr	n = *c.* 154	Brazil	Tryon, Bautista & Araujo (1975)
S. fistulosa Labill.	n = *c.* 270	New Zealand	Brownlie (1965)
S. dichotoma (L.) Smith	n = *c.* 540	New Zealand	Brownlie (1961)
Subgenus ACTINOSTACHYS			
S. pennula (Swartz) Hook.	n = 134	Trinidad	Walker (present comm.)
S. boninensis (Nakai) H. Ohba	n = 140	Bonin Island	Mitui (1973)
S. digitata (L.) Swartz	n = 325 ± 30	Sri Lanka	Lovis (in Holttum, 1959)
	n = 350 – 370	S. India	Abraham, Ninan & Mathew (1962)

2. **Lygodium** Swartz

Roy & Manton (1965) demonstrated the existence in *Lygodium* of three base numbers forming an aneuploid series, namely x = 28, 29, and 30. *L. micans* and *L. venustum* are two common Trinidad species, climbing in secondary forest, abandoned farm land or at the edge of primary forest where the light intensity is relatively high. Both species are based on x = 29, the former species being diploid with 2n = 58 (Figs 4A & 5A) and the latter tetraploid with 2n = 116 (Figs 4B & 5B). Whilst the chromosome lengths of *L. micans* show a normal distribution those of *L. venustum* clearly shows a bimodal distribution (Fig. 6A) suggesting the presence of two structurally different genomes and hence an alloploid origin of the latter species. This situation is also paralleled in members of the x = 28 series as seen in the illustration by Roy & Manton (1965) showing tetraploid *L. flexuosum* from North Borneo (2n = 112) as having chromosomes of two size classes whilst those of the diploid members were more uniform in length.

Fay (1973) reported a putative hybrid between *L. venustum* and *L. micans* from Trinidad but this was sterile and no cytological information is available for this interesting plant. A sporeling which was alleged to be of this hybrid was sent to Newcastle by A. C. Jermy but unfortunately did not survive long enough to be cytologically examined. A fully mature fertile specimen in herb. T. G. Walker was overlooked until attention was drawn to it by C. D. Adams. It had shed a golden mass of spores in its folder as do fertile species, but on examination these spores were all misshapen and obviously non-viable (Fig. 4F). It may be noted that a heavy shedding of abortive spores on this scale is most unusual in the majority of sterile fern hybrids. The hybrid clearly shows heterosis, the fertile 'pinnae' being much longer than those of either of the parental species (compare Fig. 6D with Fig. 6B & C) and the same is true of the sterile plant illustrated by Fay. This latter specimen was collected by her near Guayaguayare in south-east Trinidad, whilst T6960 came from the south-west corner at Irois. This hybrid appears not to be rare and has been named *L.* × *fayae* in honour of Dr Alice Fay. A comparison of the morphological features of the fertile fronds of *L.* × *fayae* and its parents is given in Table 4.

A species which is very similar in appearance to *L. micans* is *L. volubile* Swartz and doubts have been expressed as to whether or not *L. micans* and *L. volubile* may be synonymous. However, *L. volubile* in Jamaica at least differs from *L. micans* in Trinidad in cytology, the

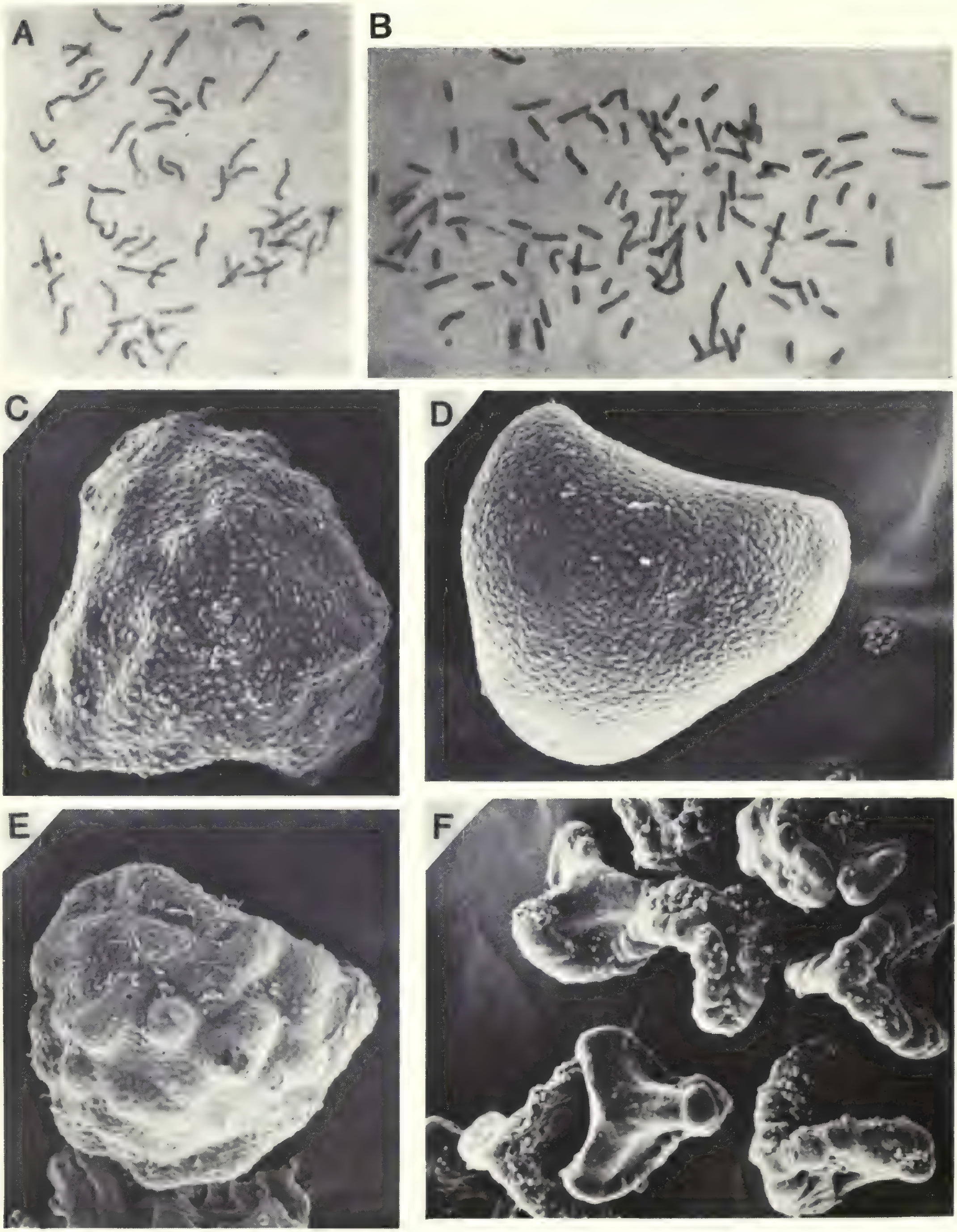

Fig. 4 *Lygodium*. **A**, *L. micans*, J1101, mitosis, 2n = 58, × 1000. **B**, *L. venustum*, J10844, mitosis, 2n = 116, × 1000. **C**, *L. volubile*, T4389 (Jamaica), spores, × 650. **D**, *L. venustum*, T6013, spores, × 650. **E**, *L. micans*, T6526, spores, × 650. **F**, *L.* × *fayae*, T6960, spores, × 300.

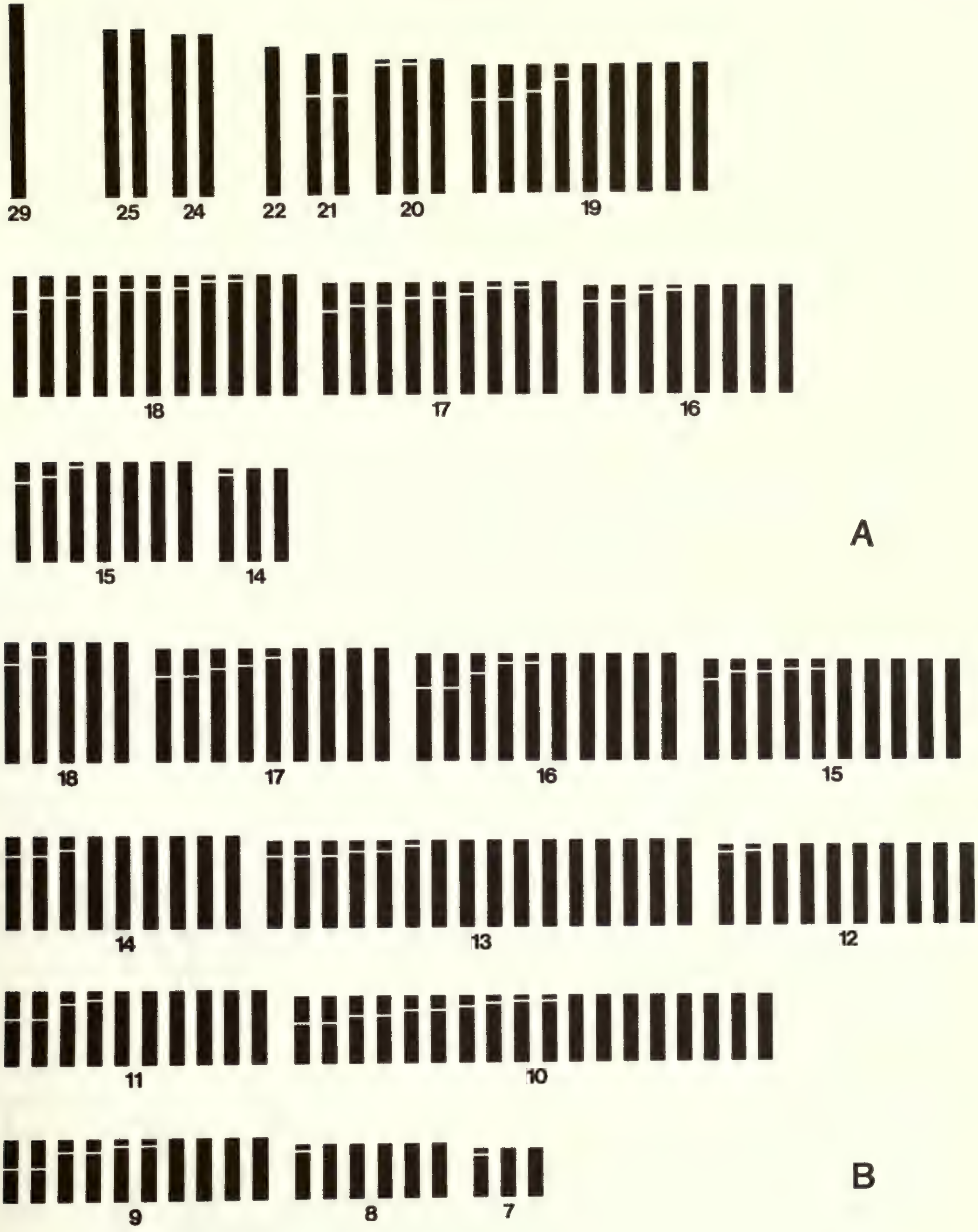
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Fig. 5 *Lygodium*. **A**, *L. micans*, J11001, karyogram, 2n = 58. **B**, *L. venustum*, J10844, karyogram, 2n = 116. Each unit of length = 0·33 μm.

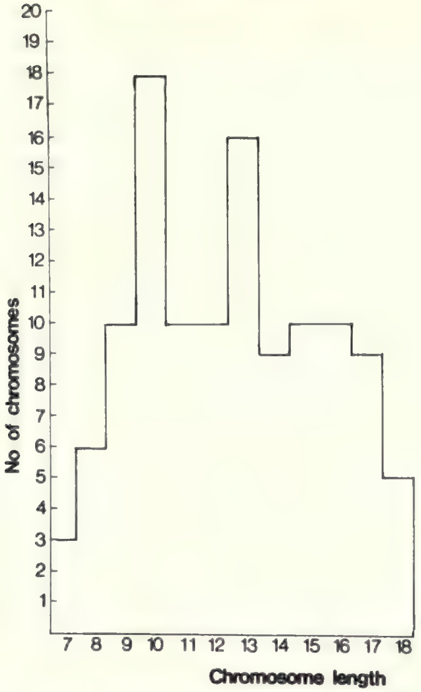

Fig. 6A *Lygodium venustum*, J10844, histogram of chromosome lengths. Each unit of length = 0·33 μm.

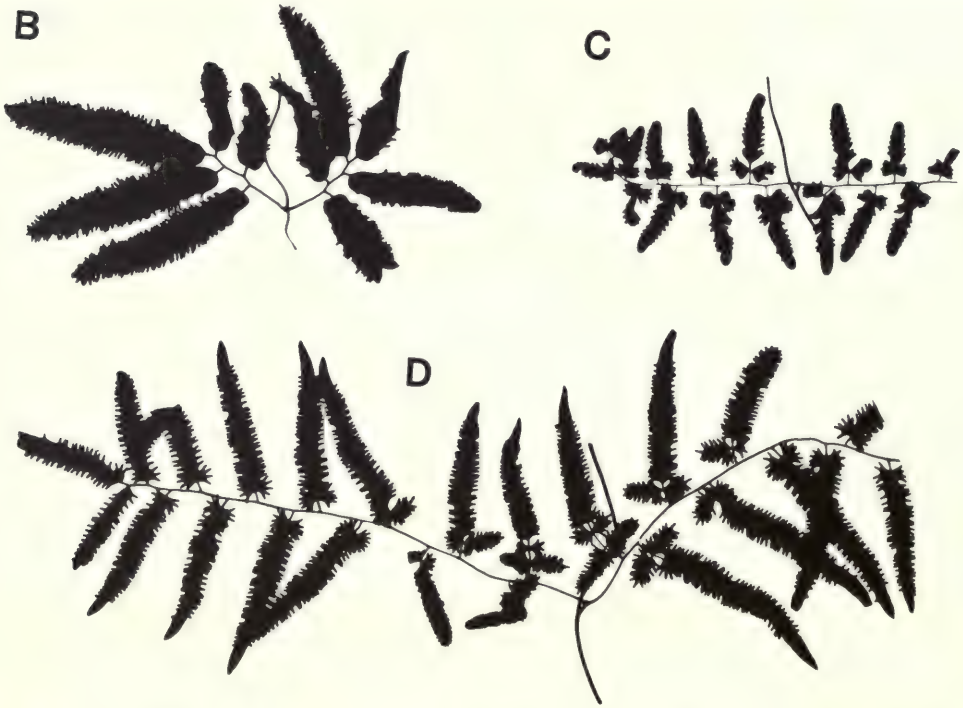

Fig. 6B–D *Lygodium*. **B**, *L. micans*, T6144, silhouette of fertile pinna, × 1/4. **C**, *L. venustum*, T6013, silhouette of fertile pinna, × 1/4. **D**, *L.* × *fayae*, T6960, silhouette of fertile pinna, × 1/4.

Table 4 Comparison of *Lygodium venustum, L. micans,* and their hybrid *L.* × *fayae*.

Character	*L. venustum*	*L.* × *fayae*	*L. micans*
1. Pinna length	short (*c.* 16 cm)	long (*c.* 30 cm)	short (*c.* 16 cm)
2. Pinnule rachis	very hairy	intermediate	more sparsely hairy
3. Number of pinnules	*c.* 6 pairs	*c.* 7 pairs	2–3 pairs
4. Pinnule dissection	deeply lobed at base or pinnate	deeply lobed at base or pinnate	entire
5. Pinnule length (L)	short (40 mm)	long (100 mm)	long (100 mm)
6. Pinnule breadth (B)	narrow (*c.* 8 mm)	narrow (*c.* 10 mm)	broad (*c.* 18 mm)
7. Pinnule L/B ratio	*c.* 5	*c.* 10	*c.* 5–6
8. Fertile segments per pinnule	few (20–40)	numerous (80–100+)	numerous (80–100+)
9. Spores	well-filled	abortive	well-filled

former being hexaploid (Walker, 1966*a*) and the latter diploid (present comm.). There are also appreciable differences in spore morphology (Fig. 4C & E). The spore morphology of these two species contrasts markedly with that of *L. venustum* (Fig. 4D).

3. **Anemia** Swartz

Two species of this predominantly American genus have been investigated from Trinidad, namely *A. phyllitidis* and *A. pastinacaria*. The former species was raised at Newcastle from spores collected from a dried specimen sent to me by Dr Alice Fay and it proved to be a sexual tetraploid with n = *c.* 76 and 2n = *c.* 152. This is in agreement with plants of this species from Mexico (Sorsa in Fabbri, 1965; Smith & Mickel, 1977) and Costa Rica (Gomez-Pignataro, 1971). Similar additional counts have been obtained from Sri Lanka, where it is an introduced species (Manton & Sledge, 1954) and from several sources of botanic garden material.

Mickel (1982) reported meiotic counts of 114 for two specimens of *A. pastinacaria* from Mexico and n = 106 and 119 respectively for a further two plants. There is a discrepancy in that, in his Table 2, Mickel shows this species as being hexaploid but in the text (p. 409) he states that the spores show some abortion, suggesting that it is a triploid apomict, at least in Mexico. In Trinidad *A. pastinacaria* proved to be a triploid agamosporous species with those spore mother cells which were destined to give rise to functional spores showing 114 bivalents at meiosis (Fig. 7C & D). Cells from other sporangia showed an irregular meiosis, the chromosomes being associated as 38 univalents and 38 bivalents (Fig. 7A & B). At maturity there was a mixture of very spinous, ridged, well-filled spores intermixed with non-functional misshapen ones, a feature which when considered in conjunction with the cytological details indicates that this is agamospory of the common Döpp-Manton type. Only one other case of agamospory has been reported in *Anemia*, namely *A. tomentosa* var. *anthriscifolia* (Schrader) Mickel and this was triploid also (Mickel, 1962).

The important contribution to the cytology of *Anemia* by Mickel (1962) in the reporting of results for 11 taxa has been overlooked by both Fabbri (1963, 1965) and Löve, Löve & Pichi Sermolli (1977) in their compilations of chromosome numbers. In all, 15 taxa, representing each of the three subgenera (*Anemia, Anemiorhiza*, and *Coptophyllum*) had been cytologically investigated and comprise diploids, triploids, tetraploids, and hexaploids. All are based on a chromosome number of x = 38, which has also been found for *Mohria* (Lovis & Roy, 1964) and contrasting with the somewhat indeterminate nature in *Schizaea* (q.v.) and the number found in *Lygodium* (x = 28, 29 and 30). Pichi Sermolli (1977) has used the distinctive chromosome number, together with other morphological evidence to separate *Anemia* and *Mohria* as a family, Anemiaceae. Similarly, he recognises Schizaeaceae and Lygodiaceae as the other components of what is usually recognised as a single family Schizaeaceae.

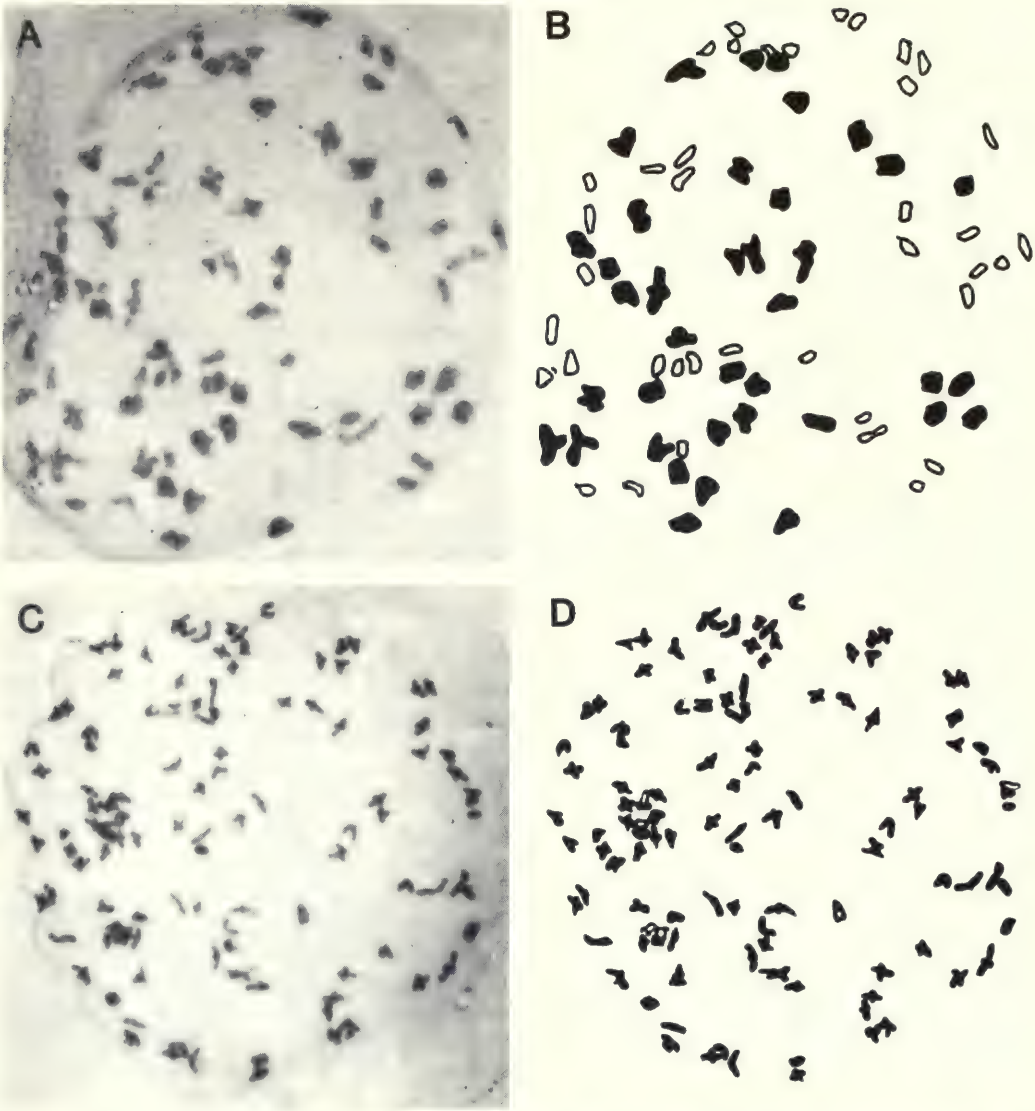

Fig. 7 *Anemia pastinacaria*, T6638. **A**, meiosis, showing 38 bivalents + 38 univalents, × 1000. **B**, explanatory diagram of A, bivalents solid, univalents outlined, × 1000. **C**, meiosis, showing 114 bivalents, × 500. **D**, explanatory diagram of C, × 500.

III. ADIANTACEAE

1. Adiantopsis Fée

Copeland (1947) includes *Adiantopsis* in *Cheilanthes* but states that it is possible to typify it by *A. radiata* and to recognise it as a small genus. In his discussion of Sinopteridaceae in which he places *Adiantopsis*, Pichi Sermolli (1977) enumerates the characters by which it clearly differs from *Cheilanthes* and places it next to that genus and *Aspidotis* in his system. Of the 15 genera assigned to Sinopteridaceae there is cytological information for nine of them and all agree in having chromosome numbers based on x = 29 or 30.

Only a single cytological record exists for *Adiantopsis* which occurred in a preliminary report (Walker, 1973*a*) for a Trinidadian plant of *A. radiata*. A root tip cell showing 2n = 60 is

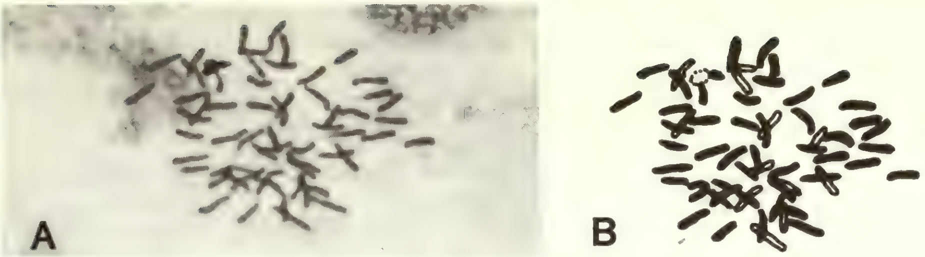

Fig. 8 *Adiantopsis radiata*, J2045. **A**, mitosis, 2n = 60, × 1000. **B**, explanatory diagram, × 1000.

illustrated in Fig. 8A & B. A further specimen, *Jermy* 10993:3, has since been examined and has confirmed this result.

2. **Pityrogramma** Link

Pityrogramma is poorly represented in Trinidad both in numbers of species and of individuals; *P. calomelanos* being the only species examined. This is a plant of open situations and has the biological characteristics of a weed. Thus it is capable of rapidly colonizing new open areas aided by its very rapid development and precocious spore production. These properties, in combination with its introduction into many countries of the world by virtue of its attractively dissected fronds and copious silvery farina, has led to its establishment in many floras on a pantropical scale. The only counts available for native American material of this genus outside the United States are those of n = 60 and *c.* 120 from Jamaica (Walker, 1966*a*) and n = 116 from Brazil (Tryon, Bautista & Araujo, 1975), these being octoploids, whilst in the United States diploids and tetraploids, together with a triploid hybrid, have been reported by Alt & Grant (1960) and diploid by Smith (1974).

In Trinidad the only specimen found in a fixable condition was exceptionally large with fronds up to *c.* 150 cm in length, three or four times that of plants collected elsewhere in the island. This was growing in a typical open situation in razor grass (*Paspalum virgatum* L.) on the edge of *Mauritia* palm forest at Aripo Savanna well removed from habitation. It had approximately 150 chromosomes associated irregularly at meiosis (as *c.* 76 univalents and 37 bivalents in one instance (Fig. 9A & B) and is a pentaploid of hybrid origin. The spores show a high degree of

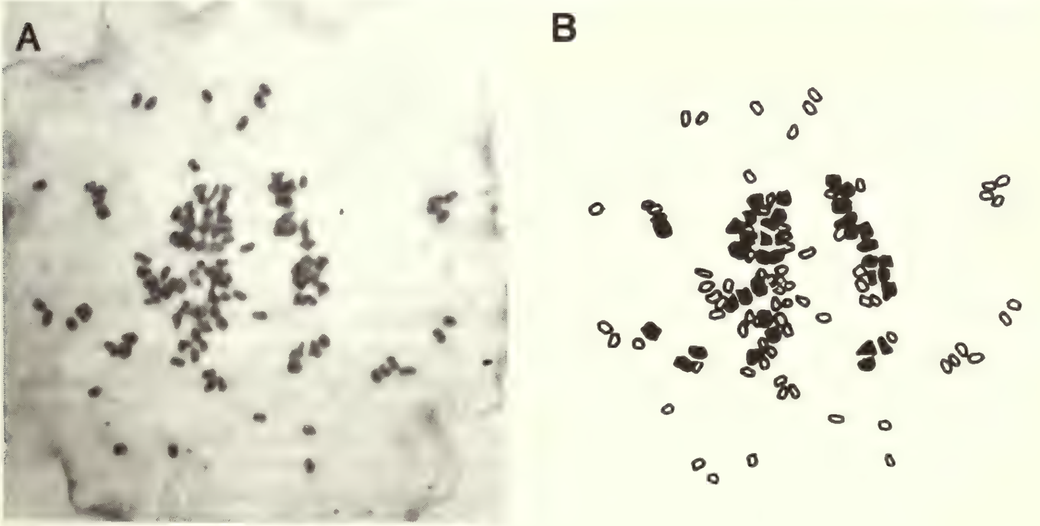

Fig. 9 *Pityrogramma calomelanos* 5x hybrid, T6354. **A**, meiosis, × 1000. **B**, explanatory diagram showing 37 bivalents (solid) + 76 univalents (outlined), × 1000.

abortion and irregular shapes but a proportion appeared to be well-filled. No other *Pityrogramma* was collected in the vicinity and its parentage is unknown, although *P. calomelanos* must be the most probable candidate for one half of the combination.

3. **Hemionitis** L.

This is a small genus of some five or six taxa in the Americas together with the disjunct and, at first sight, somewhat different *H. arifolia* (Burman) T. Moore of south-east Asia. However, Mickel (1974) has demonstrated that the differences between the American species and *H. arifolia* are more apparent than real, although Tryon & Tryon (1982) consider the latter may be related to *Syngramma* or a palaeotropical element of *Doryopteris*.

H. arifolia is agamosporous with both triploid (Abraham, Ninan & Matthew, 1962) and tetraploid (Manton & Sledge, 1954; Kurita, 1965; Matthew quoted in Fabbri, 1965) cytotypes. Both cytotypes are based on x = 30 as is also the only other species, namely *H. palmatum*, for which cytological information is available. *H. palmatum* is a diploid sexual species, its meiotic chromosome number of n = 30 being first established by Manton & Sledge (1954) on a plant of unlocalised American origin. Further material from Mexico (Wagner, 1963; Smith & Mickel, 1977), Jamaica (Walker, 1966*a*), and Costa Rica (Gomez-Pignataro, 1971) has confirmed this finding which also holds true for this species in Trinidad.

4. **Adiantum** L.

Adiantum forms a conspicuous element of the fern flora of Trinidad where it is represented by 18 species and two well-established hybrids, although this bald figure conceals a greater cytological complexity. Several of the species are common and the genus as a whole occupies a wide variety of habitats, ranging from permanently damp gullies in dense forest to open sites exposed to full sunlight and experiencing severe seasonal droughts.

Chromosome counts have been obtained for approximately half the taxa and two of the species showed more than one level of ploidy based on x = 29 or 30. The distribution of ploidy is given in Table 5 from which it will be seen that diploids predominate. *A. latifolium, A. macrophyllum, A. pulverulentum* (in part), and *A. tetraphyllum* (in part) agree cytologically with Jamaican material (Walker, 1966*a*, 1973*b*), the first two being tetraploid and the other two diploid. Araujo (in Löve, 1976) reports *A. petiolatum* as being diploid in Brazil, agreeing with Trinidadian material in this respect. The counts for all other taxa and cytotypes in Table 2 represent new records. A number of plants show unusual features that call for further discussion.

Table 5 Distribution of ploidy in Trinidadian cytotypes of *Adiantum*.

Ploidy	2*x*	3*x*	4*x*	8*x*+
No. of cytotypes	7	1	3	1

Three specimens of *A. pulverulentum*, collected from beside the trail to Maracas Falls were diploid (Fig. 10B & C) but an individual from the Forest Reserve at Brickfields in the centre of the southern half of the island differed remarkably in its cytology. This latter plant showed the very unusual number of n = 122 with all the chromosomes paired at meiosis. This count was unequivocal (Fig. 10A) and was confirmed on several cells from different preparations and must therefore be accepted as typical for this plant and not arising from the presence of a single aberrant sporangium in the fixation. An octoploid based on x = 30 which is typical of so many species of *Adiantum* would be expected to show n = 120, hence this plant with its two additional pairs of chromosomes must be regarded as a hyperoctoploid. Other deviations from numbers based on strict multiples of x = 29 or 30 have been recorded in the literature for various members of *Adiantum* (Abraham, Ninan & Mathew, 1962; Mitui, 1968; Holttum & Roy, 1965; Manton &

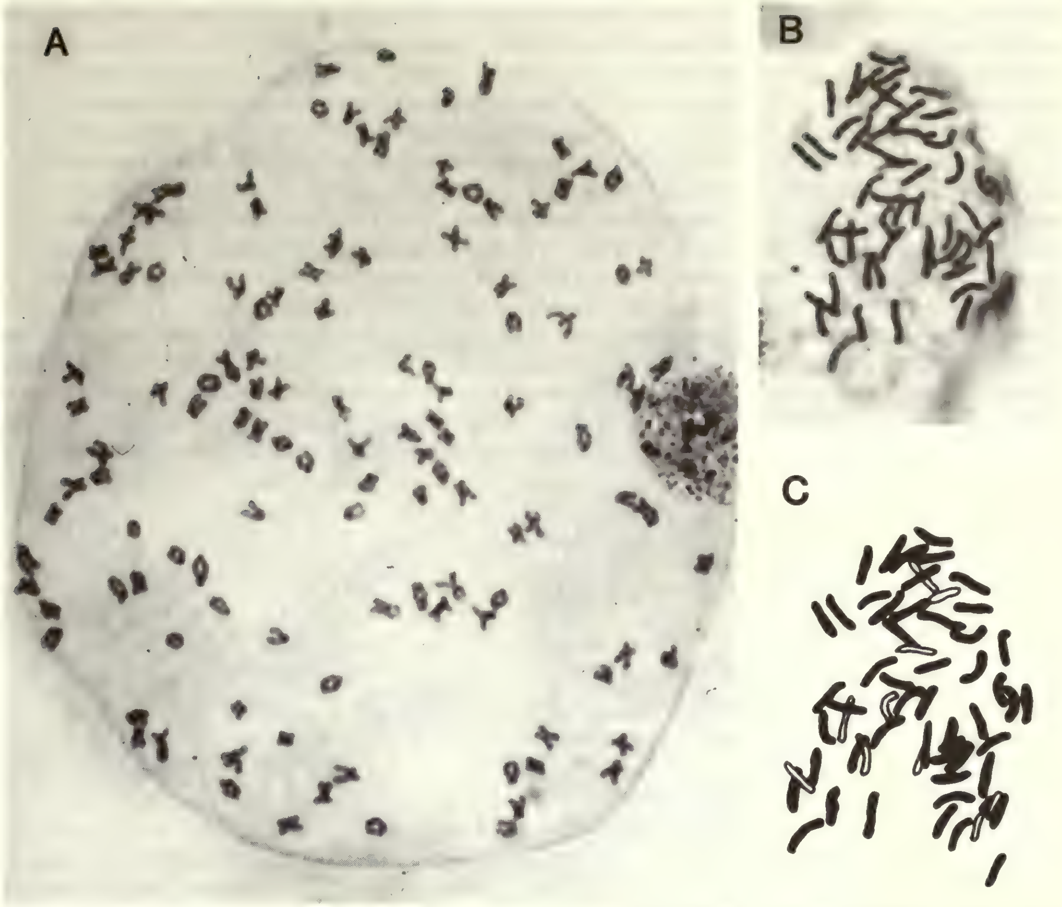

Fig. 10 *Adiantum pulverulentum*. **A**, T6614, meiosis, n = 122, × 1000. **B**, T10633, mitosis, 2n = 60, × 1000. **C**, explanatory diagram of B (a few chromosomes are completely out of focus in the photograph), × 1000.

Vida, 1968) but all have had fewer chromosomes than expected and variously rank as hypotetraploids, hypooctoploids, and hypodecaploids. *A. pulverulentum* is most remarkable in that the great difference in ploidy between the two cytotypes (2x versus *c.* 8x) is not accompanied by morphological differences, and I have been unable to distinguish between these cytotypes on any criteria other than that of chromosome number. It seems highly probable that autoploidy is involved here with suppression of multivalent formation at meiosis and a comparison of the karyotypes of the two forms would have been most instructive. However, living material is no longer available for this purpose.

A. tetraphyllum is another case in which both ploidy differences and aneuploidy occur. The single representative of this species reported from Jamaica was tetraploid and sexual in which the chromosome number could not be determined with complete accuracy and was recorded as n = 58–60, 2n = 116–120 (Walker, 1966*a*). A further Jamaican plant from a totally different locality has since been found to be tetraploid also. Eight plants have been investigated from several areas in Trinidad and Tobago, half the plants being diploid and the other half tetraploid. The two ploidies were represented in at least three different localities each, hence the conclusion is that a given cytotype is not particularly restricted in its distribution but is widespread in the country. Aneuploidy is also superimposed on the situation, small deviations from strict multiples of the base number being found in both diploids and tetraploids. Thus, the somatic numbers 2n = 114, 117 and 118 were found in three different tetraploid plants and 2n = 62 in a diploid plant. In these instances it is clear that both loss or gain of up to a few chromosomes are tolerated equally well. It may be pointed out here that although the pinnules of *A. tetraphyllum* vary considerably in morphology, ranging from shortly oblong to being much longer and with a very attenuated tip, this variation is not apparently correlated with cytological differences.

The bipinnate, tetraploid *A. latifolium* is a common fern in Trinidad and frequently grows intermixed with the simply pinnate, diploid *A. petiolatum*. Both these species have a regular meiosis, forming 60 bivalents and 30 bivalents respectively. However, five plants were collected from four different localities in the Northern Range which proved to be triploid with irregular meiosis. More detailed analyses showed a range of chromosome pairing from 22 bivalents plus 46 univalents to 30 bivalents plus 30 univalents. All these triploid plants are clearly sterile hybrids of *A. latifolium* × *A. petiolatum* and their affinity to both parents is strikingly illustrated in Fig. 11C & D which show two fully fertile fronds collected in the field from the same individual plant. Whilst one of the fronds (Fig. 11C) is simply pinnate and shows a strong resemblance to *A. petiolatum* (Fig. 11A) the other frond (Fig. 11D) is bipinnate, albeit weakly so, and is close in appearance to *A. latifolium* (Fig. 11F). Because of the variable appearance of this hybrid it is

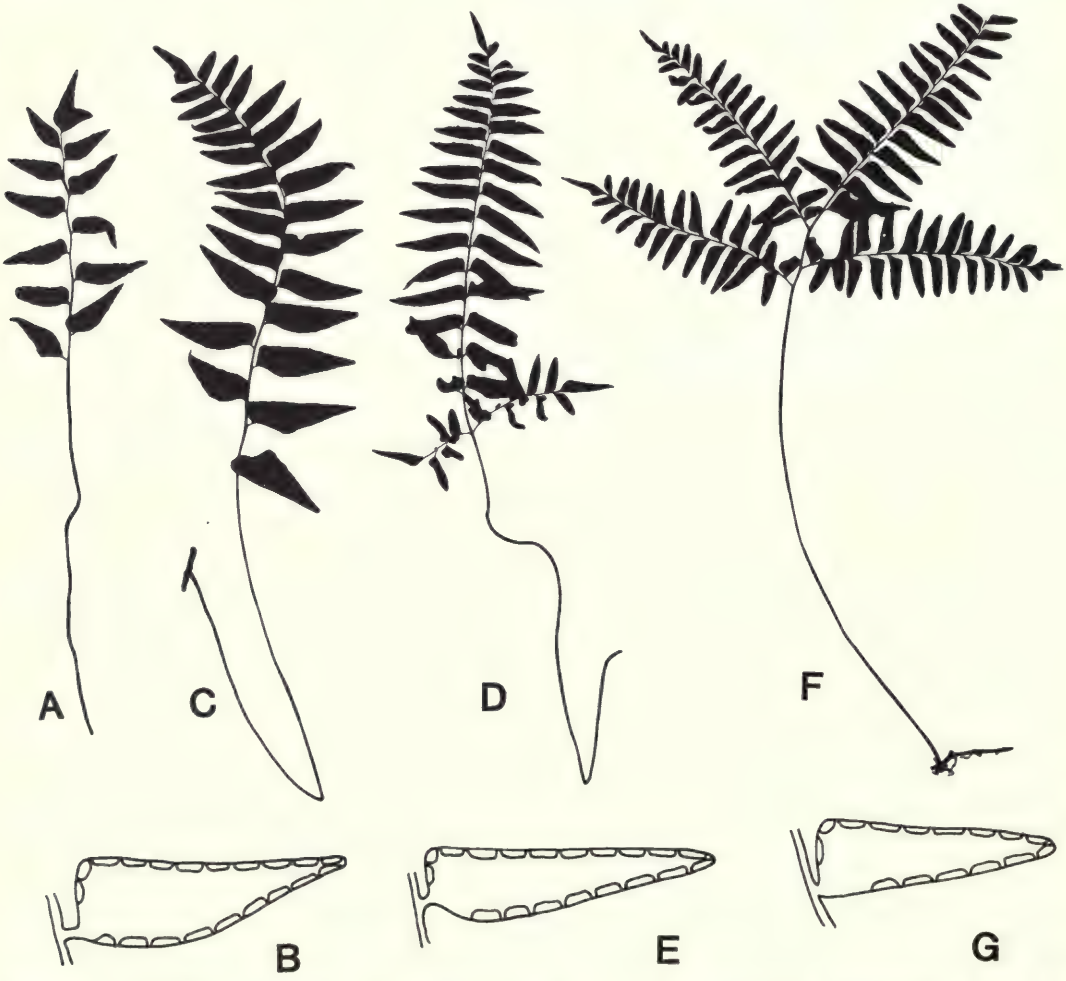

Fig. 11 *Adiantum*. **A**, silhouette of *A. petiolatum* (2x), × 1/4. **B**, pinna of *A. petiolatum*, × 1. **C & D**, silhouettes of *A.* × *variopinnatum* (3x), × 1/4. **E**, pinna of *A.* × *variopinnatum*, × 1. **F**, silhouette of *A. latifolium* (4x), × 1/4. **G**, pinnule of *A. latifolium*, × 1.

being given the name *A.* × *variopinnatum*. As has been noted above, this hybrid has been found in several localities in Trinidad and almost certainly occurs elsewhere in the Caribbean and on the mainland. Supporting evidence for this is the comment by Proctor (1977) in his *Flora of the Lesser Antilles – Pteridophyta* that the pinnae are simple in *A. petiolatum* but that rarely the basal ones are pinnate. The undersides of the fronds of *A. latifolium*, *A. petiolatum*, and *A.* × *variopinnatum* are markedly glaucous, especially in the living state, and bear numerous discrete sori on the margins in sharp contrast to the other species of *Adiantum* with which they might be confused. A comparison of the features of these three taxa is given in Table 6. Typical pinnae and pinnules are shown in Fig. 11B, E, & G.

Table 6 Comparison of *Adiantum petiolatum, A. latifolium,* and their hybrid *A.* × *variopinnatum.*

Character	*A. petiolatum*	*A.* × *variopinnatum*	*A. latifolium*
1. Rhizome	short, creeping	intermediate, creeping	long, creeping
2. Frond spacing	shortly spaced	intermediate	widely spaced
3. Pinnation	simply pinnate	simply pinnate or bipinnate	bipinnate
4. Lateral pinnae	absent	one pair only; short in comparison with terminal pinnae	up to 2 or 3 pairs ± equal in length to terminal pinnae
5. Cytology	diploid sexual, meiosis regular	triploid sterile, meiosis irregular	tetraploid sexual, meiosis regular
6. Spores	well-filled, viable	abortive, non-viable	well-filled, viable

Several species of *Adiantum* grow along the dry, exposed path-sides in the uppermost part of Lady Chancellor's Drive in the hills overlooking Port of Spain. Two of them, *A. lucidum* and *A. villosum*, proved to be sexual diploids each having 60 somatic chromosomes and a regular meiosis with the formation of 30 bivalents. Young plants which were identified in the field as *A. lucidum* were also collected from the Caura Valley and sent back to Newcastle for cultivation. These were cytologically examined on reaching maturity and all proved to be diploid but whilst some consistently showed the formation of 30 bivalents at meiosis the others showed irregular pairing. An analysis of 10 cells is presented in Table 7 and clearly shows that the pairing relationships of the chromosomes are not constant, varying from instances in which only half the chromosomes are paired to those in which only bivalents are formed. This latter pattern of behaviour allows for the possibility of a small percentage of viable spores being formed with genetical and morphological consequences that will be considered more fully later. These plants with irregular meiosis were diagnosed as being hybrids between *A. lucidum* and *A. villosum* and have been described as *A.* × *villosolucidum* (Jermy & Walker, 1985).

Immature plants of *A. lucidum, A. villosum* and *A.* × *villosolucidum* are very similar in appearance (Fig. 12 B, E, & H) not only in being simply pinnate but also in a number of other details such as the pinna shape, type of scales on the fronds, the dark green colouration, etc. However, when fully mature, *A. villosum* and *A. lucidum* differ greatly, the former being bipinnate with short pinnules and the latter simply pinnate with very long pinnae (Fig. 12A & G). There are also marked differences in the texture in that the pinnae of *A. lucidum* are markedly thick and fleshy contrasting with the thin and papery character of *A. villosum*, the hybrid *A.* × *villosolucidum* occupying an intermediate position. All have single linear sori occupying the upper and lower pinna/pinnule margins (Fig. 12C, F, & I) in contrast to the numerous discrete sori seen in the *A. latifolium–A. petiolatum* complex. This character therefore clearly distinguishes *A.* × *villosolucidum* from *A. latifolium* and *A.* × *variopinnatum* with which it might be confused (cf. Fig. 11E & G). A comparison of *A. villosum, A. lucidum*, and their hybrid is presented in Table 8.

Table 7 Analysis of meiosis in two plants of *Adiantum* × *villosolucidum*.

No. of cells	Chromosome pairing
1	30 II
2	25 II + 10 I
2	22 II + 16 I
3	19 II + 22 I
2	15 II + 30 I

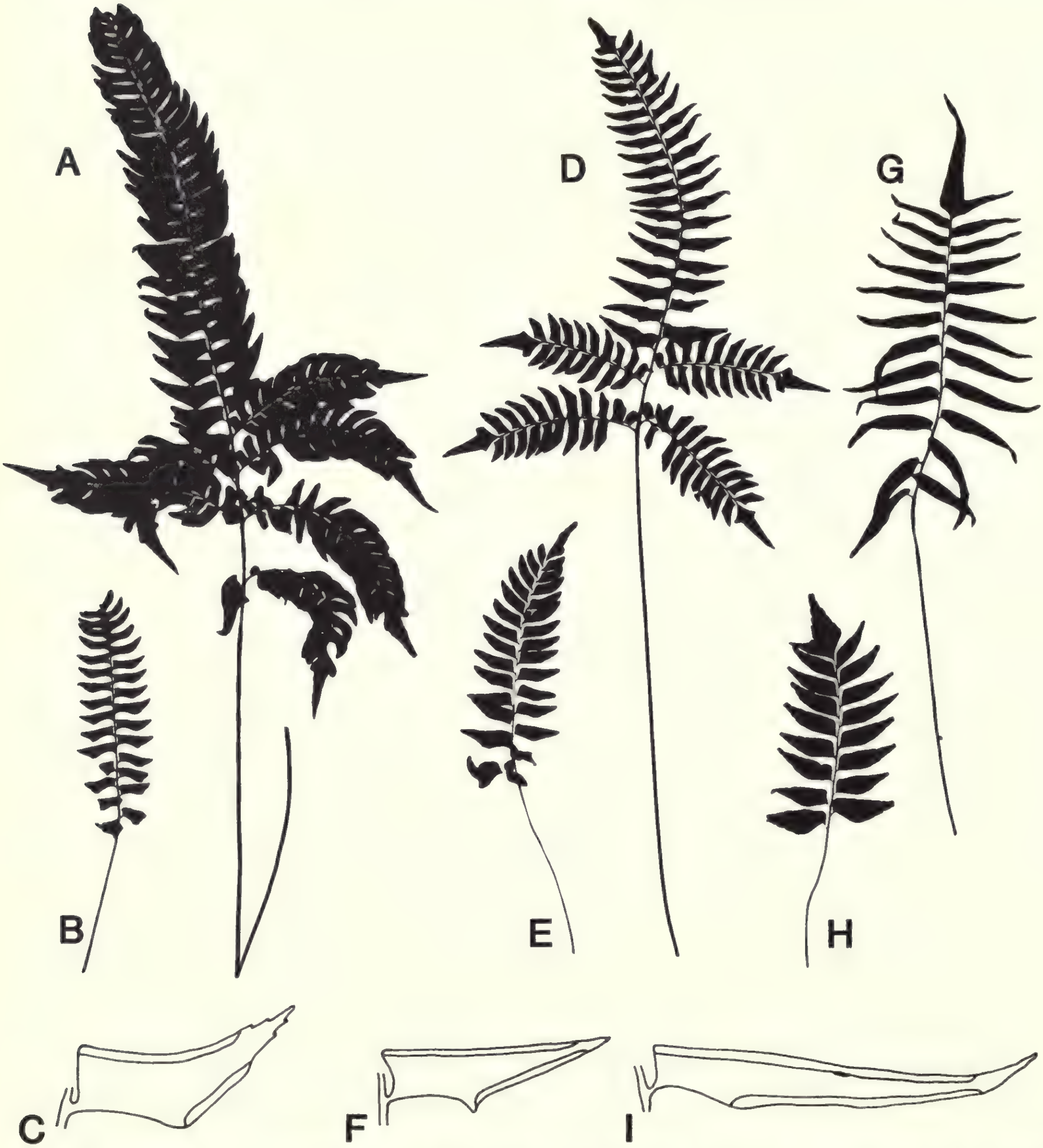

Fig. 12 *Adiantum*. **A**, silhouette of *A. villosum* (2x) mature, × 1/4. **B**, silhouette of *A. villosum*, immature, × 1/4. **C**, pinnule of *A. villosum*, × 1. **D**, silhouette of *A.* × *villosolucidum* (2x), mature, × 1/4. **E**, silhouette of *A.* × *villosolucidum*, immature, × 1/4. **F**, pinnule of *A.* × *villosolucidum*, × 1. **G**, silhouette of *A. lucidum* (2x), mature, × 1/4. **H**, silhouette of *A. lucidum*, immature, × 1/4. **I**, pinna of *A. lucidum*, × 1.

Table 8 Comparison of *A. villosum, A. lucidum,* and their hybrid *A.* × *villosolucidum.*

Character	*A. villosum*	*A.* × *villosolucidum*	*A. lucidum*
1. Pinna arrangement	bipinnate up to 6 pairs	bipinnate up to 3 pairs	simply pinnate numerous
2. Pinnules	crowded, overlapping	numerous, distant	absent
3. Texture	thin, papery	intermediate	thick, fleshy
4. Petioles	polished	polished	usually dull
5. Cytology	diploid sexual, meiosis regular	diploid sterile, meiosis mainly irregular	diploid fertile, meiosis regular
6. Spores	well-filled, viable	mainly abortive, non-viable	well-filled, viable

In cultivation *A.* × *villosolucidum* is very slow to reach full maturity, its hybrid nature in the earlier stages sometimes being betrayed by the presence of an irregularly-shaped (see Fig. 12E) or forked lowest pinna. Sometimes several years may pass before the final form is reached and indeed even after this the plant may revert to producing the simple form fronds for a period.

The two examples quoted above of naturally-occurring hybrids in *Adiantum* illustrate some of the complexities and difficulties of interpretation of a basically simple situation had there been no knowledge of the cytological background or of the behaviour of the plants in cultivation. The *A. latifolium–A. petiolatum* situation is the simplest where the two very different-looking parents give rise to a sterile hybrid which may produce mature sporangia-bearing fronds resembling either one parent or the other fairly closely, or may indeed produce both simultaneously on the same rootstock. Without this background knowledge it would be perfectly possible to classify two fronds taken from the same rhizome as belonging to the two different parental species.

The situation is more complex in the *A. lucidum – A. villosum* group. Here the fully mature fronds of both species and hybrids are strikingly different from one another but less mature fronds are all simply pinnate and look very much alike. These latter fronds may nevertheless produce sori (as is the case in 'immature' *A. villosum* in Fig. 12B) and could be mistaken for a fourth taxon. A further complication may arise out of the meiotic behaviour in the sporangia of the hybrid *A.* × *villosolucidum* (Fig. 13A–F). Here, although the large majority of the spores produced are abortive as a result of the irregularity of bivalent formation in a high percentage of spore mother cells, nevertheless some spore mother cells undergo regular meiosis and are potentially capable of producing viable spores. As a result the possibility exists that there may be introgression of genes from one species to the other on a small scale and concommitantly a further range of morphological forms due to genetic segregation. To test this possibility spores need to be sown which have been gathered from plants of *A.* × *villosolucidum* which have been grown in isolation from other members of the genus.

Taking an overall view it appears that some at least of the members of *Adiantum* are showing a cytological behaviour which is largely unfamiliar in ferns. Speciation in the case of *A. villosum* and *A. lucidum* seems to be by an accumulation of genetic differences accompanied by a much slower breakdown of chromosome homologies, such that pairing in the hybrid is not fixed but shows a variable response, and the same may be true of *A. petiolatum* and one of the parental species of *A.latifolium*. Whilst aneuploidy is often characteristic of different groups of species in a genus, e.g. in *Blechnum* with base numbers ranging from $x = 28$ to $x = 36$, each species is itself very stable and has a single chromosome number (or direct multiple). By contrast, in *Adiantum* not only may different species show deviations from exact multiples of the basic chromosome number but this may also occur *within* species. It would appear that in marked contrast to other ferns *Adiantum* is extraordinarily well-buffered against possible adverse effects of such changes, differences in chromosome numbers also being found in diploids and not just confined to high polyploids where loss or gain of a few chromosomes may reasonably be assumed to be less harmful, as in the case of *Ophioglossum, Schizaea,* etc.

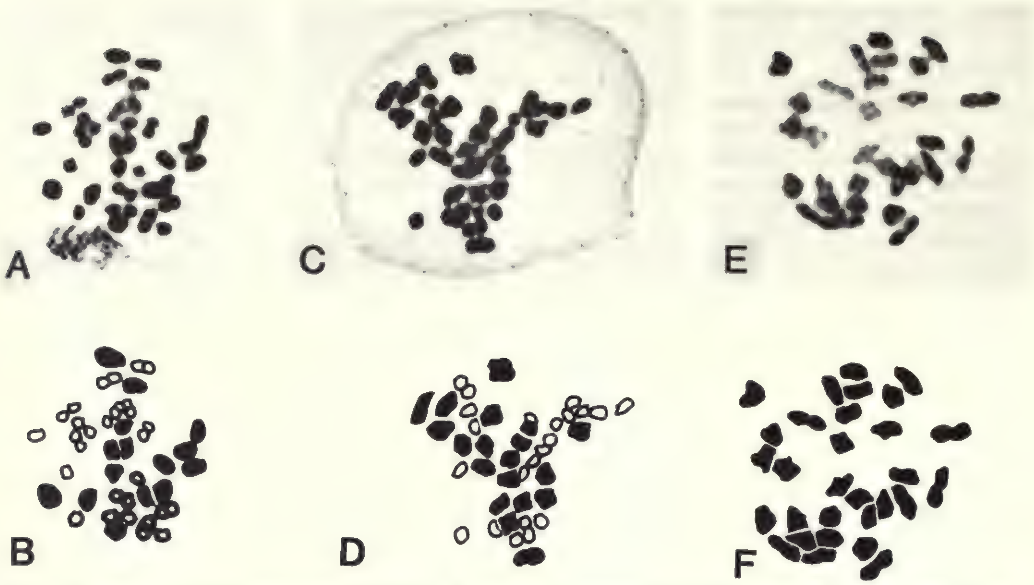

Fig. 13 *Adiantum* × *villosolucidum*, T10590. **A**, meiosis, showing 15 bivalents + 30 univalents, × 1000. **B**, explanatory diagram of A (bivalents solid, univalents outlined), × 1000. **C**, meiosis, showing 19 bivalents + 22 univalents, × 1000. **D**, explanatory diagram of C, × 1000. **E**, meiosis, showing 30 bivalents, × 1000. **F**, explanatory diagram of E, × 1000.

5. **Polytaenium** Desv.

The closeness of the relationship of this genus to the Old World *Antrophyum*, from which it differs in the presence of a costa and in the absence of paraphyses, is very clear. Indeed the only point at issue between various authors concerns whether or not the two genera should be merged. Thus, Proctor (1977) and Pichi Sermolli (1977) maintain *Polytaenium* as distinct, whilst Kramer (1978) and Tryon & Tryon (1982) do not, and assign the American species to *Antrophyum*, although the latter authors accept the group at subgeneric level. Chromosome counts are available for representatives both from the Old and the New Worlds, being variously reported under the two generic names. The basic chromosome number of 30 is present in both genera, as indeed it is in the subfamily Vittarioideae as a whole, and there is no cytological distinction to aid the taxonomy.

Two species were cytologically examined from Trinidad and both proved to be tetraploid, *P. cajenense* having n = 60 and the narrow-fronded *P. feei* having a somatic count of 2n = 120. The result for the latter species is in agreement with the report of n = 60 by Sorsa (in Fabbri, 1965; Sorsa, 1970) on Puerto Rican material. The only other counts available for this genus are from Jamaican plants (Walker, 1966*a*), these being n = 60 for *P. lineatum* (Sw.) Jenman and n = 120 for a plant reported under the name of *P. discoideum* (Kunze) Benedict but recently named by Rolla Tryon as *Antrophyum dussianum* Benedict.

6. **Anetium** Splitgerb.

This monotypic genus was reported under the name *Pteridanetium* as having a chromosome number of n = 60 (Walker, 1966*a*). This count was based on the Trinidadian plant listed here and was illustrated. It may be noted that for both *Anetium* and *Ananthacorus*, Löve, Löve & Pichi Sermolli (1977) state 'no information', whilst in fact data for both were presented in Walker (1966*a*).

7. Pteris L.

Pteris longifolia and *P. vittata* are the commonest members of a small complex centred on them. The former has a predominantly New World distribution, whilst the latter is Old World. However, the situation has been complicated by the fact that superimposed on this natural distribution there have been many introductions as decorative plants, and these species' prelidiction for open, often dry habitats has enabled them to become established in man-made habitats, such as road-banks, etc., or on rocks.

Because of their great similarity in appearance the two species have often been confused, and Jarrett (1968) pointed out that they may be distinguished from one another by the attachment of the pinnae to the rachis – in the case of *P. longifolia* the pinnae show an articulation to the rachis, whilst *P. vittata* shows no such structure and the pinna stalk is decurrent on the rachis as a ridge without constriction (Fig. 14A & B). It may be mentioned that in many specimens of *P. longifolia* the rachis is densely scaly at the junction and occasionally the articulation is not clearly seen unless the scales are removed. Proctor (1977) also pointed out that in *P. longifolia* the pinnae tend to be spreading as opposed to the ascending or oblique habit of those of *P. vittata*. This has proved to be a very useful character in Jamaican and Trinidadian material.

In Trinidad all the specimens are of *P. vittata*, it having been introduced here without, apparently, any of the New World *P. longifolia* being present. Apart from a single specimen from Grand Cayman Island (Walker, 1962) all the numerous specimens of these two species that have been examined from many different parts of the world are tetraploid and the Trinidadian material is no exception.

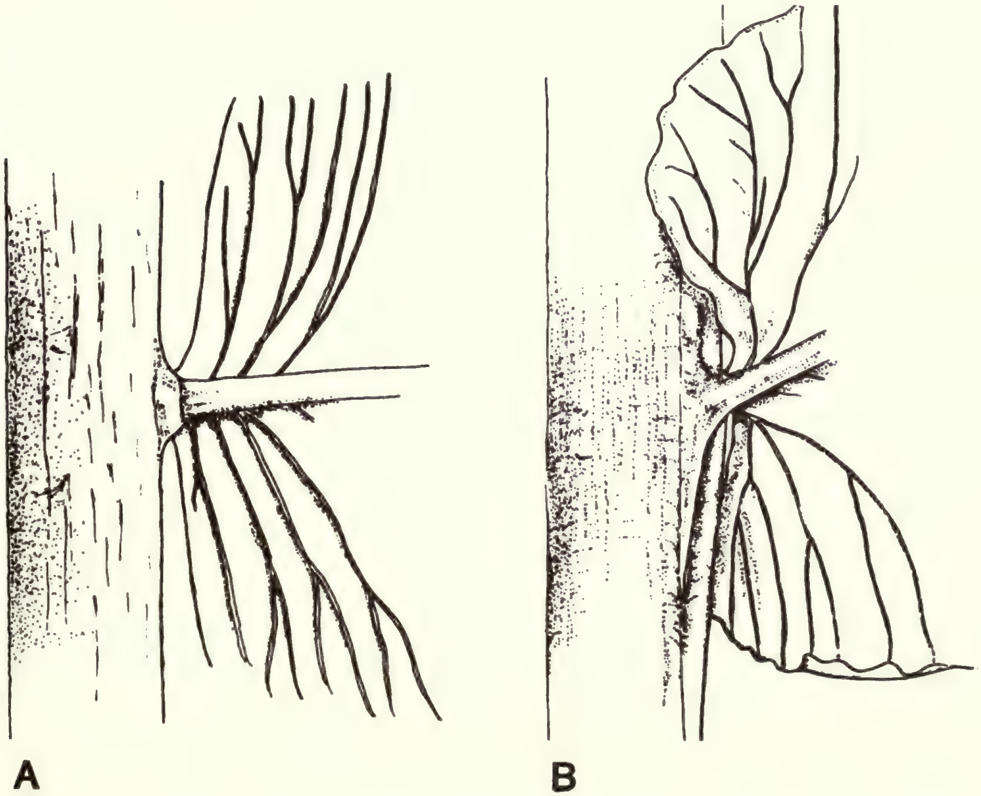

Fig. 14 Junction of rachis and pinna in *Pteris* abaxial side of frond with scales removed to show junction. **A**, *P. longifolia*, T5436 (Jamaica), × 12. **B**, *P. vittata*, T11061 (Trinidad), × 12. (Del. A. T. Pickering.)

P. tripartita is generally considered to be a widespread species native to the Old World and Pacific tropics and which has become naturalized in the Americas, although Kramer (1977) considers its alien status to be somewhat uncertain. This very large tripartite-fronded species, which has a relatively slender erect rhizome or short trunk, has been examined from three localities in Trinidad. Although differing vegetationally from one another, each locality was characterised by wet areas in which this fern grew. The young fronds secrete mucilage, as is found in a number of ferns of wet habitats. All the specimens were sexual tetraploids, as in Costa Rica (Gomez-Pignataro, 1971) and from within its undisputed natural range of Western Malaysia, Java, Papua New Guinea, and Australia (Walker, 1962).

The other two species of *Pteris* examined and for which no previous cytological records exist were also sexual tetraploids – these being *P. inaequalis* and *P. arborea*. Much confusion has existed over the latter species, in part brought about by the great size of the plant, resulting in the collecting of fragmentary specimens or the presence of unusually small or juvenile fronds in herbaria. Proctor (1977) has listed the synonymy, together with comments as to which names he thinks have been applied to juvenile plants, etc. Some idea of the size of the plant may be gained from the fact that a typical specimen had a rootstock of *c.* 45 cm in diameter, of which the greater part consisted of a mass of wiry intertwined roots. One of its fronds, which was pressed in its entirety, had a stipe *c.* 2·5 m long, surmounted by the lamina some 2 m wide. When cut up to fit the large sized fern herbarium sheets of the British Museum (Natural History) the final tally was 24 full sheets, excluding the stipe! Unlike the spores of most species of *Pteris* these proved to be of short viability and the few sporelings which were raised appeared to be intolerant of any desiccation and did not survive beyond the juvenile stage.

8. Acrostichum L.

Members of this genus are typically ferns of mangrove regions and brackish swamps along the coasts and estuaries of the tropics and subtropics. Whilst occasionally regarded as consisting of a single taxon, *A. aureum* L., this view is not universally accepted and several species are commonly recognised. In the Caribbean region there is, in addition to the pantropical *A. aureum*, the very large and distinctive *A. danaefolium*. The latter is restricted to the Western Hemisphere and is characterised by its dimorphic fronds, imbricate pinnae, and prominent irregularly sausage-shaped paraphyses. These, together with less obvious additional diagnostic features, are illustrated in Adams & Tomlinson (1979) and contrasted with those of *A. aureum*.

Two samples of *A. danaefolium* were examined from very different habitats. The first was from a large population in a typical *Acrostichum* habitat at Icacos Point on the south-west coast of Trinidad. Here the species occurred in abundance in swampy ground opening to the sea and dominated on the landward side by *Blechnum serrulatum* and *Cyperus* spp. The plants were very luxuriant, the fronds being some 3·5 m long, crowded on massive erect rootstocks *c.* 30 cm in diameter. Sporangial squashes showed $n = 30$ in spore mother cells and in addition a count of $2n = 60$ was obtained from a tapetal cell, the plant thus being a sexual diploid. A further chromosome count of $2n = 60$ was obtained from a member of a population consisting of only two, much less robust plants growing in a very different type of habitat, namely in a ditch at the edge of Aripo Savanna almost in the centre of the island and far removed from the sea (see Jermy, 1985).

The diploid chromosome counts obtained in Trinidad are in agreement with results from Jamaican material (Walker, 1966*a*) and from a plant at Kew of unknown origin (Manton & Sledge, 1954). It may be noted that no polyploid cytotypes have been reported for this genus from anywhere in the world.

IV. HYMENOPHYLLACEAE

The taxonomy of this family has been the subject of much discussion which has intensified in recent years, partially under the stimulus provided by cytology. The two most comprehensive revisions have been those of Copeland (1938, 1947) resulting in the final recognition of 34 genera in all and of Morton (1968) who, whilst only recognising six genera, nevertheless constructed a very elaborate hierarchy of infra-generic groupings. More recently Pichi Sermolli (1977) has produced a scheme which essentially follows that of Copeland, with some additional genera, bringing the number up to 42, but arranged more in line with Morton's scheme. Finally, Tryon & Tryon (1982) recognise the two classic genera *Hymenophyllum* and *Trichomanes*, the former comprising seven subgenera and the latter five.

Copeland's scheme was used in the only major survey of American Hymenophyllaceae (Walker, 1966*a*) and because so many species are common to Jamaica and Trinidad the same plan is followed here as a matter of convenience and to reduce explanatory cross references to a minimum. Similarly, for the most part discussion concerning the relationships of Copeland's genera have been kept to a bare minimum or omitted altogether as this aspect has in the main been dealt with in Walker (1966*a*), particularly for New World members and extensively by Braithwaite (1975) for Old World representatives. It is evident that the stage has been reached where the next major step forward must involve a thorough morphological study and reappraisal of the family as a whole and especially of those genera which in the past have been included in *Hymenophyllum* s.l., taking into account the indicators that cytology has provided in the course of examination of approximately a fifth of the species in the family on a world-wide basis. There is evidence that the present day chromosome numbers met with in the filmy ferns have evolved from much lower numbers relatively recently. For a fuller discussion of this see Walker (1966*a* & 1973*a*) and Lovis (1977). More recently, direct evidence has been obtained that some at least of the series in *Trichomanes* s.l. are based on $x = 9$ by the finding of the gametic number $n = 9$ in *Vandenboschia chevalieri* (C.Chr.) Kunkel by Tilquin (1978*b*). Because of this the levels of ploidy quoted in Table 2 are not absolute but are intended to enable comparisons to be easily made between one species and the next as to the relative levels. For the same reason, data for Hymenophyllaceae are usually omitted when calculating overall percentages of various levels of polyploidy in floras.

The Trinidadian species which have been cytologically examined are arranged according to Copeland's (1947) and Morton's (1968) schemes in Table 9 to enable direct comparisons to be made.

Table 9 Disposition of Trinidadian species of Hymenophyllaceae, examined in this survey, according to Copeland (1938) (which is mainly followed here) and Morton (1968).

Copeland's scheme	Morton's scheme
Mecodium polyanthos	*Hymenophyllum* subgen. *Mecodium* sect. *Mecodium*
Sphaerocionium hirsutum	*Hymenophyllum* subgen. *Sphaerocionium* sect. *Ciliata*
Vandenboschia hymenophylloides	*Trichomanes* subgen. *Trichomanes* sect. *Lacosteopsis*
Trichomanes crispum	*T.* subgen. *Achomanes* sect. *Achomanes* subsect. *Crispa*
T. polypodioides	*T.* subgen. *Achomanes* sect. *Acarpacrium*
T. fimbriatum	*T.* subgen. *Achomanes* sect. *Acarpacrium*
T. arbuscula	*T.* subgen. *Achomanes* sect. *Trigonophyllum*
T. pinnatum	*T.* subgen. *Achomanes* sect. *Neurophyllum*
Feea osmundoides	*T.* subgen. *Achomanes* sect. *Feea* subsect. *Feea*
Selenodesmium rigidum	*T.* subgen. *Pachychaetum* sect. *Pachychaetum*
Davalliopsis elegans	*T.* subgen. *Pachychaetum* sect. *Davalliopsis*
Didymoglossum angustifrons	*T.* subgen. *Didymoglossum* sect. *Didymoglossum*
*Didymoglossum kapplerianum**	*T.* subgen. *Didymoglossum* sect. *Microgonium*
Lecanium membranaceum†	*T.* subgen. *Didymoglossum* sect. *Lecanium*

* *Microgonium kapplerianum* in this paper.
† *Lecanolepis membranacea* in this paper.

1. **Mecodium** C. Presl ex Copel.

Two gatherings of *M. polyanthos* from El Tucuche were at first sight very different to one another; one (T6920) was very much smaller, the fronds being *c.* 2·5 cm high as compared with *c.*

7·5 cm of the typical form. The small plant was also less dissected and a somewhat darker green. However, they differed in no essential features and both proved to have n = 28 as did also specimens from Guanapo River Valley (quoted in Walker, 1966*a*). Proctor (1977) shows that this polymorphic species has two distinctive forms in the Lesser Antilles and all specimens in this survey belong to var. *polyanthos*.

Elsewhere this species has been examined from Jamaica (Walker in Manton & Sledge, 1954; Walker, 1966*a*), Japan (Tatuno & Takei, 1969*a*), Fiji and the New Hebrides (Braithwaite, 1975) with the same result, namely n = 28. Two deviant cases occur in the literature – one is an aneuploid from India (Mehra & Singh, 1957) with n = 27 and has been commented upon already (Walker, 1966*a*). The other case is more problematic, arising out of confusion in reporting. The number 2n = *c.* 28 was reported by Araujo (1976) for a Brazilian plant but in Löve, Löve & Pichi Sermolli (1977) this appears as 2n = *c.* 56. If the first entry is correct and its somatic number is indeed *c.* 28 it would provide the first direct confirmation of the derivation of 28 from a lower number in existing species, in this case 14, but in view of the contradiction in the reports this should be treated with the greatest circumspection pending further information.

2. **Sphaerocionium** C. Presl

S. hirsutum is a widespread tropical American species and lectotype of the genus (Pichi Sermolli, 1977). Three gatherings in Trinidad showed n = 36, with a perfectly regular meiosis as had also a further four gatherings in Jamaica (Walker, 1966*a*). Two other collections, however, from different localities in the Northern Range in Trinidad also had approximately 72 chromosomes but these showed irregular behaviour at meiosis indicative of a hybrid nature. Although accurate analyses were not possible the majority of the chromosomes were present as univalents but a number of bivalents also occurred. The hybrid plants, *S.* × *tucuchense*, found on El Tucuche growing very close to *S. hirsutum*, are in general appearance (see Jermy & Walker, 1985: Fig. 5) very similar to *S. hirsutum* and it seems most likely that this is one of the parents involved. The relatively simple construction of a filmy fern does not in general provide many obvious characters for determining the identity of the less dominant parents in hybrids, but in this case several features of use have been noted and it seems probable that *S. elegans* Sprengel (= *S. cruegeri* (C.Mull.) Copel.) is the other parent. Unfortunately, the chromosome number of this species is not known. A comparison of the two species and the hybrid is given in Table 10.

Table 10 Comparison of *Sphaerocionium hirsutum, S. elegans*, and putative hybrid (*S.* x*tucuchense*).

Character	*S. hirsutum*	*S.* x*tucuchense*	*S. elegans*
1. Frond habit	± stiff and erect	± stiff and erect	soft and pendulous
2. Lamina	stellate hairs conspicuous on veins	stellate hairs conspicuous on veins	stellate hairs, few on veins
3. Rachis	winged to base	winged to base	not winged at base
4. Stipe:			
(a) wings	winged to base	winged in top ½ or 2/3, not below	not winged
(b) hairs	stellate hairs throughout	stellate hairs on winged portion; increasing % of simple hairs intermixed unwinged portion until entirely simple at base	stellate hairs at top, increasing % of simple hairs intermixed until entirely simple at base
5. Cytology	n = 36, meiosis regular	72 chromosomes, irregular meiosis	not known

3. **Vandenboschia** Copel.

V. hymenophylloides was recorded (Walker, 1966*a*) as having n = 36 from a gathering on Aripo Heights; a second gathering from El Tucuche showed the same result and is in agreement with Jamaican material.

The chromosome numbers of 17 taxa of this genus from many different parts of the world are available (literature in Löve, Löve & Pichi Sermolli, 1977) and are all based on 36 with the exception of a very important group of African species to be discussed later. A further member which proved to be cytologically anomalous (Walker, 1966*a*) namely *V. scandens* with n = 64 has latterly been removed from this group by both Morton (1968) and Pichi Sermolli (1977). The former author believing this to be the type species of *Trichomanes* places it by itself in section *Trichomanes* of subgenus *Trichomanes* whilst Pichi Sermolli firmly believing *Trichomanes* must be typified by *T. crispum* L. erected the monotypic genus *Mortonopsis* to accommodate it. *V. scandens* provides a striking example of how cytological evidence has helped to draw attention to anomalies and to the need for a closer taxonomic appraisal. The chromosome number also shows the close relationship of this species to others accepted in the genus *Trichomanes* where a base number of x = 32 is found, although Morton (*l.c.*) was mistaken in believing the base number to be x = 17. Cytologically it is no way intermediate between that genus and *Vandenboschia* as Pichi Sermolli suggests (1977: 420).

Tilquin (1978*b*) has examined four species of *Vandenboschia* in Africa of which two have what may be regarded as conventional chromosome numbers in that *V. mettenii* (C.Chr.) Kunkel showed n = 36 and *V. goetzii* (Hieron.) Kunkel showed n = 36 in one cytotype and n = 72 in another. However, *V. melanotricha* (Schlechter) Pichi-Serm. showed several different cytotypes with n = 27, 36, 54 and 72, indicating quite clearly a series based on n = 9. Direct confirmation of this base number was provided by *V. chevalieri* (C.Chr.) Kunkel which in addition to an apomictic cytotype with 'n' = 36 and a sexual one with 17 IIs + 2 Is also had a rare sexual cytotype showing n = 9, thus directly confirming that some at least of the n = 36, 72, etc., series are derived from a basic chromosome number of x = 9. A precautionary note should perhaps be sounded that the apparent x = 36 series in the filmy ferns as a whole may not be monophyletic and the possibility at least exists that there may be two series – one based on x = 9 and the other on x = 12.

4. **Trichomanes** L.

Whilst all of the five species and one hybrid examined here are included in Copeland's concept of *Trichomanes* they are arranged in Morton's classification under subgenus *Achomanes* where there is a wide spread of sections to which he has assigned them. Thus *T. crispum* (and hybrid) are in section *Achomanes, T. polypodioides* and *T. fimbriatum* in section *Acarpacrium, T. arbuscula* in section *Trigonophyllum,* and *T. pinnatum* in section *Neurophyllum*.

T. crispum has been shown to have n = 128 on a number of plants from Jamaica (Walker, 1966*a*, 1973*b*) and the same is true for a specimen from El Tucuche. All these examples had a regular meiosis. However, a further plant from El Tucuche which was initially identified as this species was in fact a hybrid having a total of 192 chromosomes instead of 256 and with an irregular meiosis. On analysis one cell showed 61 bivalents and 70 univalents, whilst another had 67 bivalents and 58 univalents. Closer morphological inspection suggests that *T. robustum*, also in section *Achomanes*, may be the other partner involved in the formation of this hybrid. In the comparison set out below (Table 11) the observations are based on Trinidadian material of *T. crispum* and the hybrid but Jamaican material of *T. robustum* has had to be utilized as I did not collect the latter species in Trinidad. Both these species are probably at the centres of complexes and in the absence of more precise data it is not proposed to name the hybrid.

One specimen of *T. polypodioides* from Trinidad was reported (Walker, 1966*a*) as having n = 64, 2n = 128 and this has been confirmed on a further specimen from a different locality. Another member of section *Acarpacrium, T. fimbriatum*, had somewhat sticky chromosomes which made absolute certainty impossible but approximately 64 bivalents were counted. Proctor (1977) has reduced this species to a variety of *T. trigonum* Desv., but Kramer (1978) has retained

Table 11 Comparison of *Trichomanes crispum, T. robustum,* and putative hybrid.

Character	*T. crispum*	hybrid	*T. robustum*
1. Rhizome	short decumbent or erect	short decumbent	long creeping
2. Rhizome hairs	long	long	short
3. Fronds	tufted	tufted	distant
4. Frond segments	overlapping, inrolled	spaced, flat	spaced, flat
5. Lamina hairs:			
a) abaxial	long (*c.* 2 mm) hairs abundant on all veins and margins	intermediate hairs (*c.* 1·5 mm) abundant on all veins	short hairs (1 mm or less) on all veins and margins
b) adaxial	abundant on all veins	hairs sparse, mainly on main vein of segment	very sparse, mainly on main veins of segment
6. Indusial tube	flared, inserted	flared, intermediate	not flared, exserted
7. Rachis	very hairy on both surfaces	very hairy on underside, less so on upper	less hairy
8. Cytology	n = 128 (? 8x), meiosis regular	192 chromosomes (? 6x), meiosis irregular	n = 64 (? 4x), meiosis regular

it as a full species on the grounds that the group as a whole contains several critical species which require further study.

T. arbuscula was collected from the ground in palm forest at the edge of Aripo Savanna and had n = 64 (Walker, 1966*a*). Tryon, Bautista & Araujo (1975) record n = *c.* 128 for *T. arbuscula* from Brazil, thus having twice as many chromosomes as the Trinidad material. However, it is clear from their photograph of this plant that it is quite different in its dimorphic habit and very long petiolate fertile fronds from the Trinidadian specimens which agree with the diagnosis given by Posthumus (1928) and Kramer (1978) for Surinam material of this species.

T. pinnatum is one of only three species comprising section *Neurophyllum* of subgenus *Achomanes*. Morphologically it is a very distinct plant with its pinnate frond combined with scattered cross-veinlets which may or may not connect adjacent veins, and the flagelliform viviparous tips to the fronds. It is remarkable in its behaviour in that it has an extremely wide range of habitat tolerance, ranging from a typically filmy fern habitat of shade and high humidity to being equally at home in such situations as roadside banks, exposed to full sun for much of the day and without showing signs of wilting or shrivelling. Two plants were cytologically examined and showed n = 32. Araujo (1976) gives the approximate count of n = *c.* 36 for this species but without any indication of the degree of latitude in the estimate. More problematical is Bierhorst's (1975) record of n = 26 but other evidence suggests the species counted is not in fact *T. pinnatum*.

5. **Feea** Bory

This small genus of some three to five species has been considered by Copeland (1947) to be closely related to *Trichomanes crispum* with which it agrees in a number of characters including the possession of chromosome numbers based on 32 or multiples.

Four Trinidadian specimens, all from the same locality and assigned to *F. osmundoides*, had, however, irregular pairing of the chromosomes at meiosis, the 64 chromosomes forming associations ranging from 10 bivalents plus 44 univalents to 13 bivalents plus 38 univalents (Fig. 15A & B), indicating a hybrid origin of the plants. By contrast Jamaican specimens (Walker, 1966*a*) also had 64 chromosomes but these regularly formed 32 bivalents at meiosis. Superficially the Jamaican species and the Trinidadian hybrids are very similar to one another and it is not

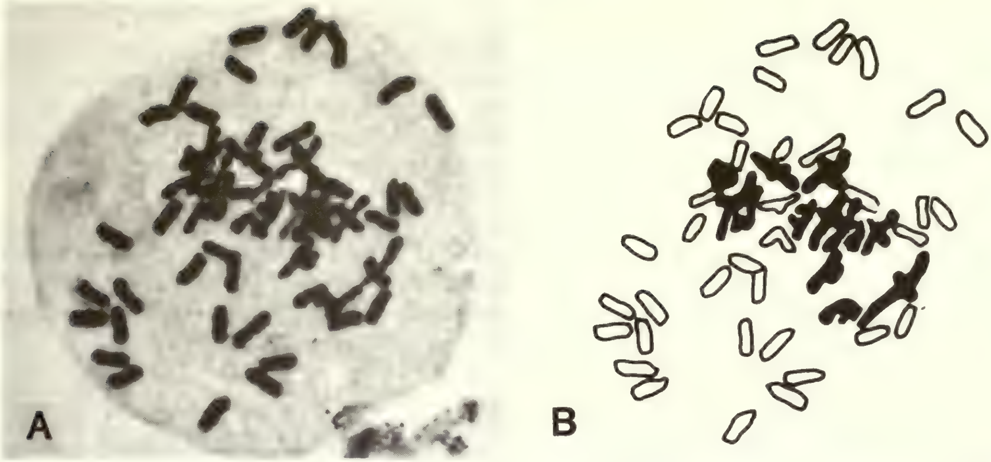

Fig. 15 *Feea osmundoides* hybrid, T6555. **A**, meiosis, 13 bivalents + 38 univalents, × 1000. **B**, explanatory diagram (bivalents solid, univalents outlined), × 1000.

possible to suggest with any degree of confidence the other species involved with *F. osmundoides* in the formation of the hybrid. Cleared fronds showed some differences in the density and type of hair, the venation, etc. Thus the Jamaican plants have conspicuous uniseriate hairs some 7–10 cells long on the underside of the rachis, somewhat shorter hairs on the underside of the main veins, and very short ones (*c.* 2 cells long) on the other veins. The veins tend to be once-forked between the base and midway along the segment. This contrasts with the Trinidadian specimens in which not only do the veins tend to be twice-forked but the hairs on the rachis and main veins are much shorter than in the Jamaican examples. On other veins there are short 2-celled hairs, the terminal cells of which are rounded. In both instances dimorphism is taken almost to the ultimate in that, whilst the sterile fronds are foliose and deeply pinnatafid, the fertile ones consist essentially of stipe and rachis with a row of stalked involucres situated in two rows, one on either side of the rachis which lacks foliose tissue.

6. **Selenodesmium** (Prantl) Copel.

The only member of this genus from the New World to be examined is *S. rigidum* which shows n = 33 in both Jamaica and Trinidad (Walker, 1966*a*), apart from a report by Araujo (1976) which needs confirmation of n = *c.* 28 in *S. cellulosum* (Klotz.) A. Löve & D. Löve. This species has been reported as having double the number, with n = 66, in Africa (Tilquin, 1978*b*). Elsewhere n = 33 has been recorded for *S. cupressoides* (Desv.) Copel. from Ghana (Walker in Manton, 1959), in *S. dentatum* (Bosch) Copel. from the New Hebrides, Fiji, and New Caledonia (Braithwaite, 1975) and *S. obscurum* (Blume) Copel. from a wide geographical area including Malaysia (Manton, 1954), Sri Lanka (Manton & Sledge, 1954), Japan (Mitui, 1968) and the Solomon Islands (Braithwaite, 1969). Apart from the unconfirmed report by Araujo mentioned above there are two other anomalous ones, that of Brownlie (1965) who quotes n = 36 for *S. dentatum* from New Caledonia in disagreement with the n = 33 recorded from 11 localities by Braithwaite. A probably more fundamental divergence is the n = 36, 2n = 72 of *S. elongatum* (Cunn.) Copel. from Queensland by Vessey & Barlow (1963). All of these species are included by Morton in *Trichomanes* subgenus *Pachychaetum* section *Pachychaetum*.

S. guineense (Afzel. ex Swartz) Pichi-Serm. was reported as being of hybrid origin by Tilquin (1978*b*) with a total of 99 chromosomes but associated irregularly as univalents, bivalents, and trivalents. Another, unidentified species again showed irregular pairing, including multivalents, but with a total of 104 chromosomes, whilst another representative of the same species had 2n = 100–105 and was apomictic.

7. **Davalliopsis** Bosch

This monotypic genus deservedly bears the specific name *elegans,* with its very large, stiffly erect fronds which show a distinct metallic, blue sheen when seen in the forest, similar to that found in various species of *Selaginella*. It is not known whether or not this sheen is of the same schemochromic origin described for *Selaginella wildenowii* (Desv.) Baker by Fox & Wells (1971) in which the blue colouration is optical and not pigmentary in origin, being caused by the differential reflection of light from a 'beaded' cell surface.

Walker (1973*a*) reported n = 32 for this species in Trinidad as did also Tryon, Bautista & Araujo (1975) from Brazilian material. This genus is placed by Morton (1968) in the same section *Feea* of *Trichomanes* subgenus *Achomanes* as is also *Feea* itself, the very large differences between them being only accorded subsectional recognition – *Hymenostachys* and *Feea* respectively.

8. **Didymoglossum** Desv.

The three species of this predominantly American genus which have been previously cytologically investigated were from Jamaica (Walker, 1966*a*, 1973*b*), these being *D. lineolatum* Bosch and *D. punctatum* Poiret (Desv.) with n = 34 and *D. kraussi* (Hook. & Grev.) C. Presl, with n = 68. A further species, *D. angustifrons*, has also the same base number, showing n = 34 clearly. This latter taxon is sometimes confused with *D. pusillum* auct. non (Swartz) Desv. which is common in Trinidad, but my specimens agree very closely with Wessels Boer's (1962) description of the former species and material named by him in the British Museum herbarium. All four species are placed by Morton (1968) in *Trichomanes* subgenus *Didymoglossum* section *Didymoglossum*.

D. liberiense (Copel.) Copel. from Zaïre has n = 34 (Tilquin, 1978*a*).

9. **Microgonium** C. Presl

Only four species of this genus are American, the vast majority being of Old World distribution. *M. hookeri* (C. Presl) C. Presl from Jamaica has n = 68 (Walker, 1966*a*) and this is true also of *M. kapplerianum* from Trinidad. This number has been recorded elsewhere in the world for *M. ballardianum* (Alston) Pichi-Serm. from Zaïre (Dujardin & Tilquin, 1971; Tilquin, 1978*a*) and in *M. bimarginatum* Bosch from Australia (Vessey & Barlow, 1963) and from Fiji (Braithwaite, 1975). It is evident that these are polyploid members, n = 34 having been found in *M. tahitense* (Nadeaud) Tindale from the New Hebrides (Braithwaite, 1975) and in *M. motleyi* Bosch from Malaya (Manton, 1954; Manton & Sledge, 1954) and the Solomon Islands (Braithwaite, 1969). This latter species has double this number in the Himalayas (Mehra & Singh, 1957).

In Africa a complex situation has been reported by Tilquin (1978*a*) in three species. In the simplest of these, *M. aerugineum* (Bosch) Pichi-Serm. from Zaïre showed a slight deviation in having 67 IIs + 2 Is at meiosis and a normal sexual reproduction, whilst another population was hybrid. However, the other two species between them showed a range of chromosome numbers which involved very high levels of ploidy and also a range of breeding behaviour. Thus *M. erosum* (Wallich) C. Presl in a population from Zaïre showed 2n = 204 and apomictic reproduction whilst other specimens from Nigeria had counts of 2n = 117–126, 2n = 193 and 'n' = 197. Similarly, *M. chamaedrys* (Taton) Pichi-Serm. had plants with n = 68 and sexual reproduction, others with 39 IIs + 10 Is (hybrids) and yet others with 'n' = 209, 'n' = 479 (apomictic), 2n = 166 and 2n = 168. It will be noted that in these cases the high polyploids are usually not exact multiples of the basic chromosome number, a situation met with most commonly in *Adiantum* (q.v.).

Wessels Boer (1962) treats this group as a subgenus of *Didymoglossum* whilst Morton (1968) arranges the species in section *Microgonium* of subgenus *Didymoglossum* of *Trichomanes*.

10. Lecanolepis Pichi-Serm.

L. membranacea is the sole member of this genus that has been cytologically examined. Jamaican specimens (Walker, 1966*a*) were sexual with n = 34, 2n = 68 and the same gametic number has been found in Trinidadian material. Morton (1968) places this species by itself in section *Lecanium* of subgenus *Didymoglossum*.

V. GLEICHENIACEAE

Gleichenia Smith **and Dicranopteris** Bernh.

Gleichenia sensu lato was split by Holttum (1959) into two genera, *Gleichenia* and *Dicranopteris*, and this treatment has been followed by Tryon & Tryon (1982). The former consists of the subgenera *Gleichenia, Diploterygium,* and *Mertensia,* whilst *Dicranopteris* comprises the sub-

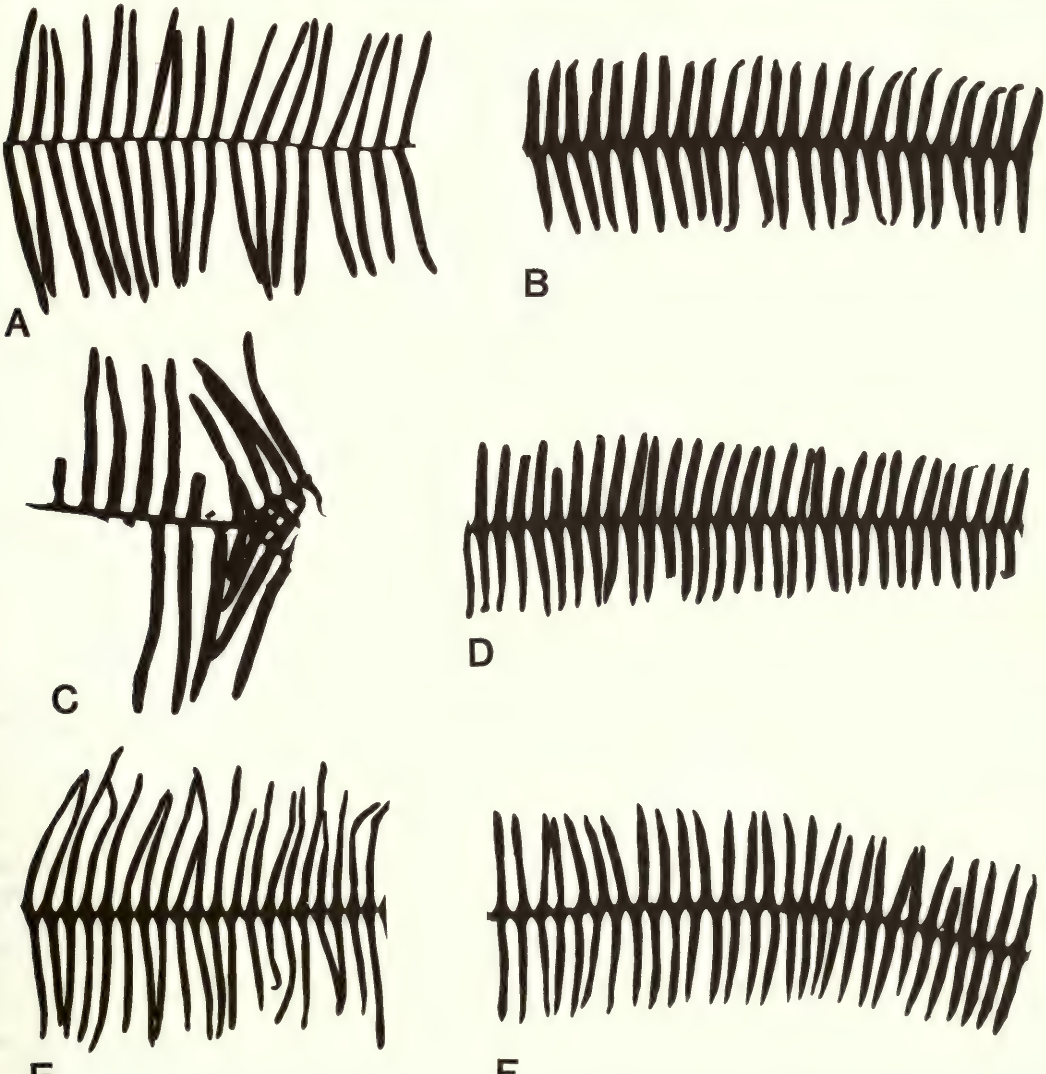

Fig. 16 *Gleichenia*, silhouettes of portions of lamina branches, × 1/2. **A**, *G. remota* (2x). **B**, *G. bifida* (2x). **C**, *G. interjecta* (4x), basal portion. **D**, *G. interjecta* (4x) more distal portion. **E**, *G.* × *subremota* (3x). **F**, *G.* × *pseudobifida* (3x).

genera *Dicranopteris* and *Acropterygium*. Reviews of the cytological results published for the genus (Walker, 1966*a*, 1973*a*, 1973*b*) show that a different basic chromosome number is characteristic of each of the five subgenera and this helps to emphasise their distinctness. The only Trinidadian representative of *Dicranopteris* for which results were obtained is *D. pectinata*. This species belongs to subgenus *Acropterygium* and is indeed the sole representative of the group. All nine specimens from four different localities in the Northern Range, showed n = 43 quite clearly, as was also the case for the Jamaican plants (Walker, 1966*a*: plate 1, Fig. 8). All the other members of Gleicheniaceae which have been examined from Trinidad belong to subgenus *Mertensia* of *Gleichenia*.

The most restricted member of this group is *G. brittonii* which is confined in Trinidad to the higher peaks of the Northern Range. It was originally described as being endemic but Duek (1971) reports this species as also occurring in Cuba. My specimen came from the type locality at the summit of El Tucuche where it grows along the pathside in an exposed position. This was diploid and showed the basic chromosome number of 34 characteristic of *Mertensia*.

G. bifida and *G. remota* (together with *Dicranopteris pectinata*) frequently grow intermingled in various proportions to form thickets of these sun-loving ferns which are such common features of leached roadside embankments. Cytological sampling was carried out at several localities and it rapidly became apparent that the situation was far more complex than appeared on casual inspection, and that there were a number of additional entities superficially resembling one another. The most distinctive of these plants is *G. remota* which is predominantly South American in distribution. It can be distinguished from all other members of the thickets by its slender habit, purplish-brown axes, light green lamina, long remote lamina segments (Fig. 16A), and its almost glabrous nature. The scales which protect the apical bud are narrow and have short stout hairs on their margins (Fig. 17A). This species is diploid with n = 34.

The most common element in the thickets is *G. bifida*, which in contrast to *G. remota* is a very robust plant with ultimate lamina branches which are only *c.* 5 cm wide (Fig. 16B). The underside of the lamina segments are densely covered with light brown scales which give the plant a characteristic brown velvety appearance beneath. The scales protecting the apical buds of the fronds are typically very wide at the base and are fringed with numerous very long hairs (Fig. 17C). This species forms not only the dominant element in the *Gleichenia* thickets but also has a much wider geographical range than *G. remota*, extending throughout the islands of the Caribbean and over much of tropical South America. Jamaican (Walker, 1966*a*, 1973*b*) and Puerto Rican (Sorsa, 1968) plants agree with the Trinidadian material in being diploid with n = 34.

A specimen from a roadside bank in the Aripo Valley was identified at the time of collection as *G. bifida* but on cytological examination it proved to be tetraploid. The preparations are unfortunately not satisfactory for photographic purposes as the chromosomes overlap and lie in different focal planes. However, despite these drawbacks one is illustrated (Fig. 19C) for the purposes of discussion. Under the microscope the chromosomes can be seen to be completely paired and to form 68 bivalents. A further feature of importance is that the bivalents are not all of approximately the same size as in the other species, some being markedly smaller than others (see bivalents arrowed in Fig. 19D). This feature will be returned to later when considering some hybrids but at this point it is sufficient to note that the presence of bivalents of two sizes in this tetraploid is a strong indication that we are dealing with an allotetraploid and not an autotetraploid showing multivalent suppression. On morphological grounds the probable parentage of this plant involves *G. bifida* and *G. remota*, followed by a doubling of the chromosomes of the initial sterile diploid hybrid. Whilst the plant has the general appearance and robustness of *G. bifida*, more detailed examination shows features characteristic of *G. remota*. The most obvious of these is in the lamina branch width and details of the lamina segments, both of which show a gradation from being typical of *G. bifida* at the more distal ends (Fig. 16D) to being typical of *G. remota* towards the basal part of the rachis branches (Fig. 16C). The apical bud scales are intermediate in width between those of *G. bifida* and *G. remota* and, whilst they have the very prominent fringe of hairs (fibrillae) as in the former species, these are not so long (Fig. 17D). Similarly, the density of the indumentum of hairs or scales on the ultimate rachis and the under

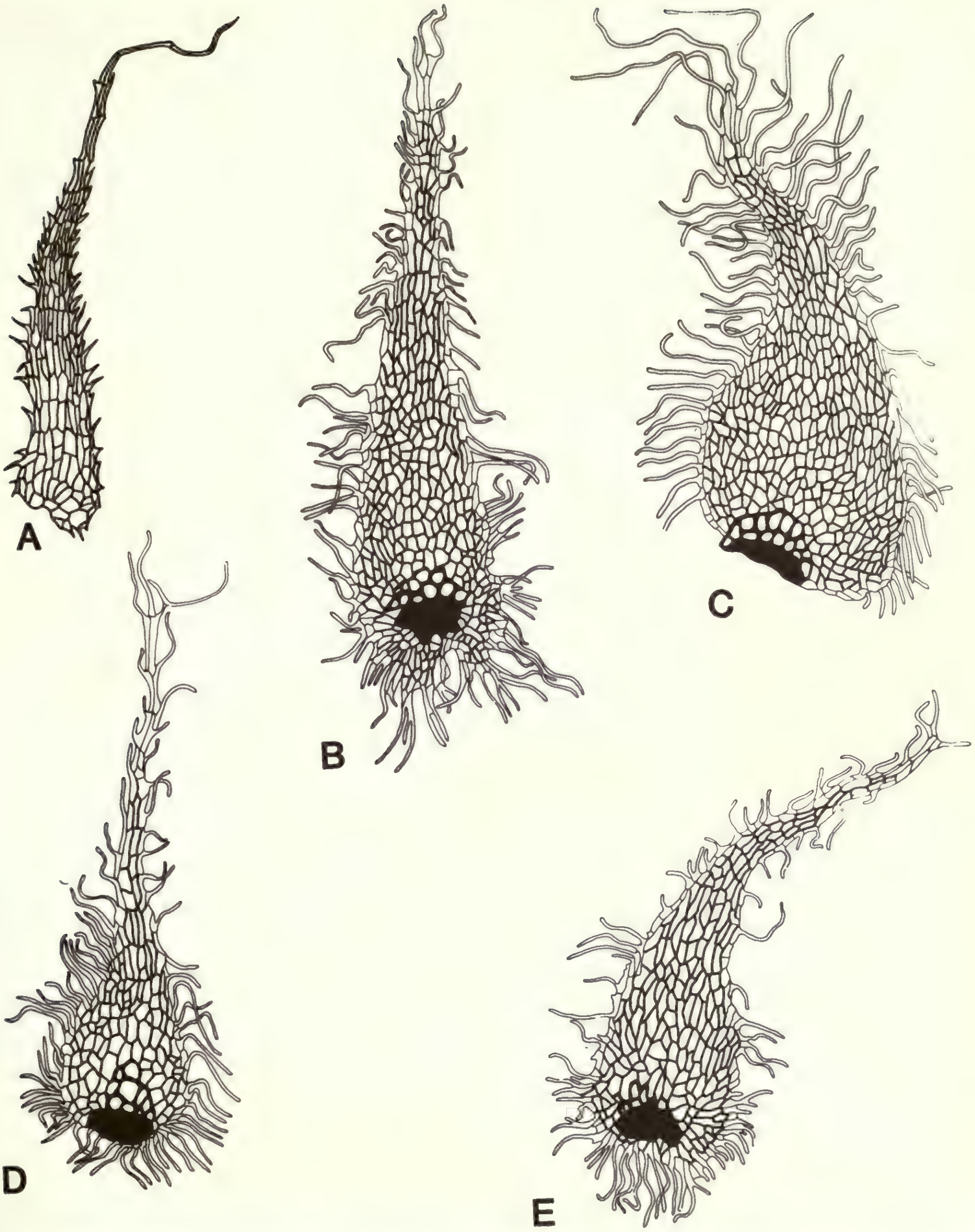

Fig. 17 *Gleichenia,* apical bud scales, × 40. **A**, *G. remota* (2x). **B**, *G.* × *pseudobifida* (3x). **C**, *G. bifida* (2x). **D**, *G. interjecta* (4x). **E**, *G.* × *subremota* (3x).

surface of the lamina segments tends to be intermediate (Fig. 18, Table 12). In view of its intermediate position this tetraploid is given the name *G. interjecta* (Jermy & Walker, 1985).

An outstanding result of the sampling of the thickets was the relatively high proportion of plants found which were triploid and showed an irregular meiosis (Table 2). These plants occurred intermixed with *G. bifida, G. interjecta, G. remota,* and *Dicranopteris pectinata* and again were at first assumed to be *G. bifida*, which they resemble (Fig. 16F). They may, however,

Table 12 Comparison of members of the *Gleichenia bifida-remota* complex.

Character	*G. bifida* (2x)	*G. interjecta* (4x)	*G. remota* (2x)
1. Ultimate rachis			
(a) adaxial surface	abundant white hairs and arachnoid scales	± naked on mature parts	naked
(b) abaxial surface	light coloured scales – not prominent (Fig. 18B)	few hairs, scattered narrowish, brown, toothed scales (Fig. 18C)	naked except for few dark brown scales (Fig. 18A)
(c) colour	greenish brown	red-brown	purplish
2. Lamina, abaxial surface	light-coloured hairs abundant, appearing as brown velvet to naked eye (Fig. 18B)	light-coloured hairs present, not so abundant as in *G. bifida* (Fig. 18C)	virtually naked (Fig. 18A)
3. Costa, abaxial surface	light-coloured scales present, not very obvious	light brown scales present, not abundant but conspicuous	sparse light brown scales present
4. Apical bud scales	broadly ovate triangular, pale red-brown; with fimbriate margins; with conspicuous basal attachment (Fig. 17C)	narrowly ovate triangular, dark red-brown with more scarious fimbriate margins than in *G. bifida* (Fig. 17D)	triangular, dark brown, toothed rather than fimbriate (Fig. 17A)
5. Lamina segments	contiguous throughout all lamina branches; *c.* 35 × 3 mm (Fig. 16B)	remote on secondary lamina branches, contiguous on ultimate branches; 35(–50) × 3 mm (Figs 16C & D)	remote throughout all lamina branches; *c.* 50 × 2 mm (Fig. 16A)
6. Outline of ultimate lamina branches	broadest near (but not at) base	widest at base, decreasing regularly	widest at base, decreasing regularly
7. Stipe colour	greenish brown	cinnamon-brown, becoming purplish at base	brown, becoming purplish at base
8. Lamina texture	harsh	harsh	soft
9. Stomatal length	$\overline{\mathrm{M}}$ 31·5 μm (26·0 to 34·0)	$\overline{\mathrm{M}}$ 43·5 μm (37·5 to 49·0)	$\overline{\mathrm{M}}$ 36·5 μm (34·0 to 41·0)
10. Cytology	2x, regular meiosis	4x, regular meiosis	2x, regular meiosis

be distinguished from this species by the relative density of the covering of hairs or scales on the ultimate rachides and undersurface of the lamina segments (Fig. 18). This feature is intermediate between that shown by *G. bifida* and tetraploid *G. interjecta* as are also the shapes of the apical bud scales (Fig. 17B) and the length of the stomata (Tables 12 & 13). The morphology, chromosome number, and cohabitation are in agreement with these plants being triploid hybrids between *G. bifida* and tetraploid *G. interjecta*, i.e. a backcross between *G. interjecta* and one of its parents.

This hypothesis is further confirmed by a study of meiosis which shows approximately equal numbers of relatively large bivalents and of exceptionally small univalents (Fig. 19A & B). This size difference is very much greater than is accounted for by the fact that a normal bivalent of two chromosomes is being compared with a univalent consisting of a single chromosome and reflects a fundamental difference, there being two size classes of chromosomes present. It will be

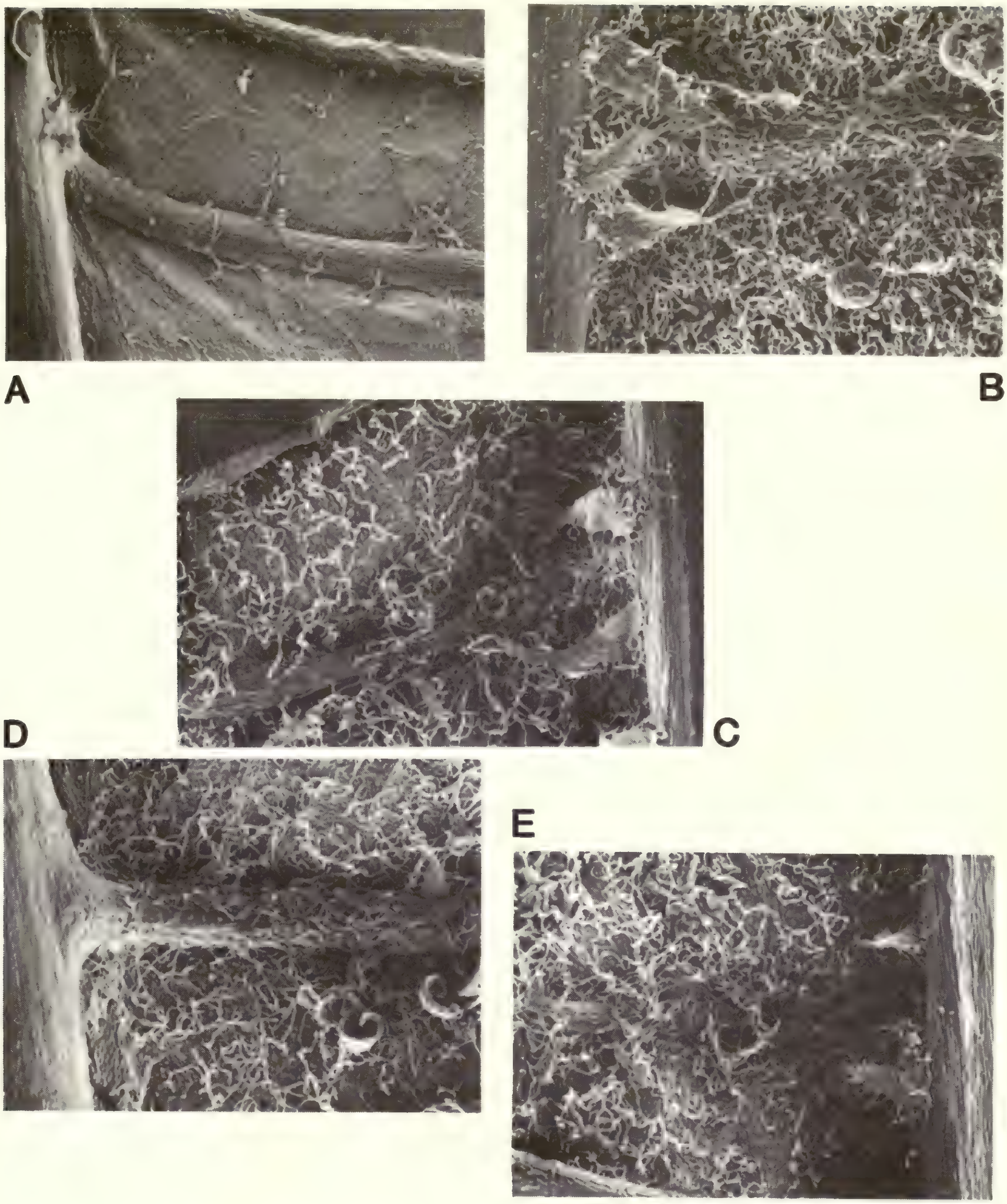

Fig. 18 *Gleichenia bifida-remota* complex. Underside of lamina segments showing indumentum on lamina and ultimate rachides. **A**, *G. remota*. **B**, *G. bifida*. **C**, *G. interjecta*. **D**, *G.* × *subremota*. **E**, *G.* × *pseudobifida*. All × 18.

recalled that *G. interjecta* had chromosomes of two sizes and, since there is very strong evidence that this triploid hybrid is *G. bifida* × *G. interjecta* and since *G. interjecta* is an alloploid, the large pairs in the hybrid must be contributed by the *bifida* genome which is here represented twice and the small univalents by the *remota* genome. Because of its similarity to *G. bifida*, this hybrid has been named *G.* × *pseudobifida* (Jermy & Walker, 1985).

One of the triploid plants, however, did not agree in morphological details with the other hybrids and showed a much stronger resemblance to *G. remota* (Fig. 16E), especially in the

Table 13 Comparison of hybrids of the *Gleichenia bifida–remota* complex.

Character	*G.* × *pseudobifida* (3*x*)	*G.* × *subremota* (3*x*)
1. Ultimate rachis		
(a) adaxial surface	white hairs present – sparser than in *G. bifida*	naked
(b) abaxial surface	prominent scales; few hairs (Fig. 18E)	almost naked – few small hairy scales at junction with costae (absent in old parts) (Fig. 18D)
(c) colour	greenish brown on under side, purplish brown on upper side	purplish both sides
2. Lamina, abaxial surface	light-coloured hairs, fairly abundant (Fig. 18E)	light-coloured hairs, fairly abundant (Fig. 18D)
3. Costa, abaxial surface	frequent light brown scales present	whitish scales present, not conspicuous
4. Apical bud scales	narrow-triangular medium brown, fringed with hairs (Fig. 17B)	triangular, purplish brown with pale fimbriate margins (Fig. 17E)
5. Lamina segments	remote at extreme base of ultimate lamina branches and below; 25(–60) × 3 mm (Fig. 16F)	continguous on ultimate but remote on lower lamina branches; 20–40 × 2–3 mm (Fig. 16E)
6. Outline of ultimate lamina branches	tapering from base	tapering from base
7. Stipe colour	pale brown or cinnamon	purplish
8. Lamina texture	harsh	harsh
9. Stomatal length	$\bar{M}$ 37·5 μm (34·0 to 41·0)	$\bar{M}$ 37·0 μm (34·0 to 41·0)
10. Cytology	3x, irregular meiosis	3x, irregular meiosis

colour of the stipes and branches and in the indument of the ultimate rachides. This specimen was considered to be the backcross of *G. interjecta* to its other parent, *G. remota*, and has been distinguished as *G.* × *subremota* (Jermy & Walker, 1985). If this was indeed the case then, in view of the dimorphism of the chromosomes noted above, this hybrid, with its approximately equal numbers of bivalents and univalents, should show the reverse of the situation seen in the other hybrids and have relatively small bivalents and very large univalents, the former being

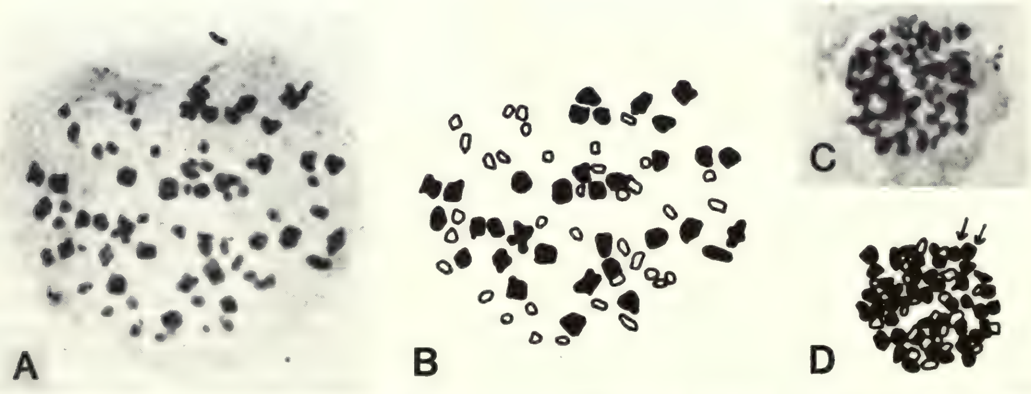

Fig. 19 *Gleichenia*. **A**, *G.* × *pseudobifida*, T6417 (3x), meiosis, × 1000. **B**, explanatory diagram, 34 bivalents (solid) + 34 univalents (outlined), × 1000. **C**, *G. interjecta* T10332 (4x), × 1000. **D**, explanatory diagram, all bivalents. Arrows point to a large and to a small bivalent, × 1000.

contributed by the two *remota* genomes present and the latter by the single *bifida* genome. This, indeed, was found to be the case, the univalents being almost as large as the bivalents, making analysis quite difficult. Unfortunately, staining in these preparations was poor and the cells could not be photographed. Finally, it should be possible to compare directly the chromosome sizes of the two basic diploid parental species *G. bifida* and *G. remota*. Unfortunately, this was not possible as no mitotic material was available, and comparisons between meiotic chromosome size are only valid when they occur in the same cell as above in the triploid hybrids and in *G. interjecta*.

One plant remained which did not agree with any of the members of the complex described above and which nevertheless showed characters of both diploid species. Unfortunately, this was not fertile and in the absence of cytological evidence it has been tentatively diagnosed on morphological grounds alone as the hybrid *G. bifida* × *G. remota*. This would be expected to be diploid and of the basic type of hybrid from which *G. interjecta* arose by chromosome doubling.

The Gleichenias of Trinidad have proved to be a classic example of an apparently simple situation of a few distinct species but which on closer examination have proved to be in reality a complex of basic diploid types with derivative allotetraploid and backcross hybrids in all combinations. A comparison of the taxa is presented in Tables 12 and 13.

Finally, it may be noted that the influence of the *G. remota* parent in all three derivative taxa (*G. interjecta, G.* × *pseudobifida*, and *G.* × *subremota*) is seen in the very long narrow lamina segments and in their wide spacing. Both these characters may be found on each of the taxa to varying degrees, the remoteness of the segments being confined to the secondary rachis branch in *G. interjecta* as a regular feature and is also usually (but not invariably) present in *G.* × *pseudobifida* in the same position. In the only specimen of *G.* × *subremota* found, the wide spacing of the segments is more widespread and reaches to about half way along the ultimate branches.

The situation in *Gleichenia* may be summarised as follows:

(i)	2x		2x		2x		4x
	G. bifida	×	*G. remota*	→	(sterile hybrid)–×2	→	*G. interjecta*
	BB		RR		BR		BBRR
	34 II's		34 II's				68 II's
(ii)							
	2x		4x		3x		
	G. bifida	×	*G. interjecta*	→	*G.* × *pseudobifida*		
	BB		BBRR		BBR		
	34 II's		68 II's		34 II's, 34 I's		
(iii)							
	2x		4x		3x		
	G. remota	×	*G. interjecta*	→	*G.* × *subremota*		
	RR		BBRR		BRR		
	34 II's		68 II's		34 II's, 34 I's		

VI. POLYPODIACEAE

1. **Dicranoglossum** J. Smith in Seeman

This small genus of ferns with forked fronds bearing submarginal coenosori at the distal ends was previously considered to consist of a single species, widely known by the later illegitimate name, *Eschatogramme furcata* (L.) C.Chr. In his study of polypodioid genera with longitudinal coenosori Christensen (1929) recognized four species, one of which (*E. furcata*) was further split into four varieties.

F. S. Wagner (1980) has recorded n = 36 for *D. panamense* (C.Chr.) Gómez (= *D. polypodioides* (Hook.) Lellinger) from Costa Rica. A Trinidadian specimen of *D. desvauxii* which has anastomosing veins as opposed to the free veins of the former species, showed n = *c.* 72 (Fig. 20A & B) and is thus a tetraploid. However, a specimen of *D. desvauxii* at Kew and

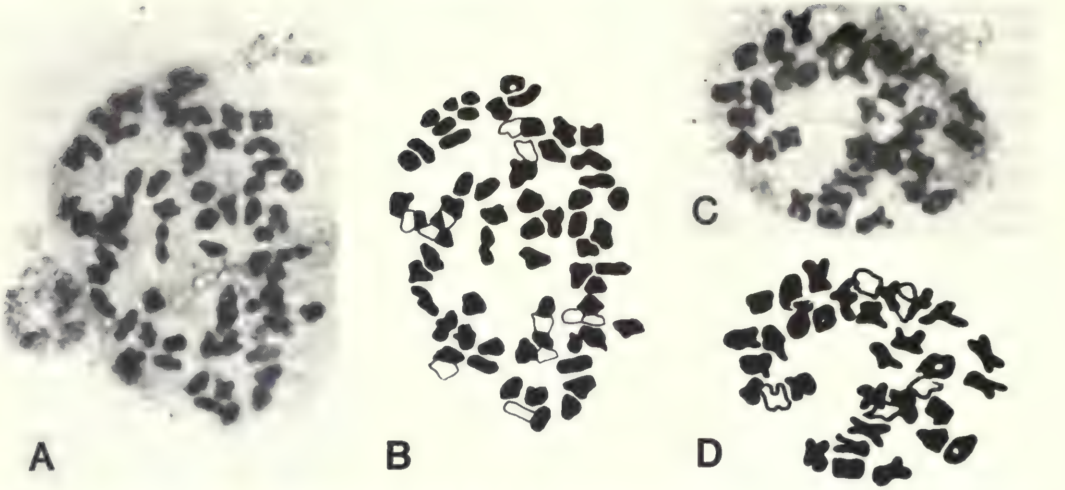

Fig. 20 *Dicranoglossum desvauxii*. **A**, T7076, from Trinidad, meiosis, n = *c*. 72, × 1000. **B**, explanatory diagram, all bivalents, × 1000. **C**, hort. Kew. from Brazil, meiosis, n = 36, × 1000. **D**, explanatory diagram, all bivalents, × 1000.

originating from Brazil had 36 bivalents at meiosis and is illustrated here (Fig. 20C & D) to record that both diploid and tetraploid cytotypes are found in this species.

In his revision of the genus Christensen (1929) considers that *Dicranoglossum* (under the name *Eschatogramme*) and *Pleopeltis* are sister genera derived from *Marginaria*-like ancestors and Copeland (1947) also concludes that except for the absence of paraphyses he would feel safe in deriving it from *Pleopeltis* and this opinion is endorsed by Tryon & Tryon (1982). Pichi Sermolli (1977) has placed the 63 genera of his Polypodiaceae into 14 groups and although stating that *Dicranoglossum* is *incertae sedis* puts it between the groups of *Polypodium* and *Pleopeltis* although nearer to the latter. Crabbe et al. (1975) also place it in the subfamily Pleopeltoidea and thus the consensus of opinion is for a relationship with *Pleopeltis*. The cytological data also give some support to this view in that x = 36 is an uncommon base number amongst New World genera belonging to *Polypodiaceae* sensu stricto and *Pleopeltis* shows a large aneuploid series of basic chromosome numbers in which x = 36 features, viz. x = 22, 23, 25, 26, 35, 36, 37, 47.

2. **Polypodium** s.l.

Polypodium s.l. is a large cosmopolitan group comprising in excess of a thousand species. Various schemes have been proposed to split it into smaller, more natural and convenient groupings but at present no thoroughly satisfactory system has emerged and the whole super-genus is in need of careful monographic study on a world basis. Several of the genera that have been split off, e.g. *Phlebodium* and *Polypodium* s.s., hybridize with one another and in other cases, such as *Goniophlebium* and *Polypodium* s.s., the differentiating characters are not always maintained. In order to provide a more convenient framework for discussion, but without implying final taxonomic judgement, in the following account the species are dealt with as members of various subgenera of *Polypodium*.

Subgenus *Polypodium*

Four plants of *P. triseriale* have been examined from two different localities in Trinidad. Two grew in the old leaf bases of *Mauritia* palms in Aripo Savanna whilst at Blanchisseuse one was on a rock and the other on a palm trunk. In each case they were diploid with n = 37, 2n = 74 (Fig. 22A), agreeing with a plant from Mexico (Smith & Mickel, 1977). However, these records contrast with those for Jamaica (Walker, 1966*a*) which were tetraploid with n = 74. Morphologically the Jamaican and Trinidadian plants are very similar indeed, agreeing in most respects, although pinnae of the Trinidadian plants tended not to be so conspicuously adnate. On the microscopic level the similarities are even more remarkable, sparsely-distributed 2-celled hairs being present on the abaxial surfaces of both cytotypes and, despite the different levels of ploidy, the stomatal lengths are virtually identical – the mean length for a Trinidadian diploid specimen being 52 μm (min. 45 μm, max. 54 μm), whilst that of a Jamaican tetraploid was 51·5 μ (min. 41 μm, max. 54 μm). Unfortunately, no living material of the tetraploid is available to compare its karyotype with that of the diploid.

P. loriceum differs from the other members of the group examined in having a thin rhizome, bearing only scattered scales. In the living state the rhizome is glaucous, becoming distinctly silvery on drying. Like the Jamaican representative (Walker, 1966*a*) this plant is also diploid with n = 37, 2n = 74 (Fig. 21A, B).

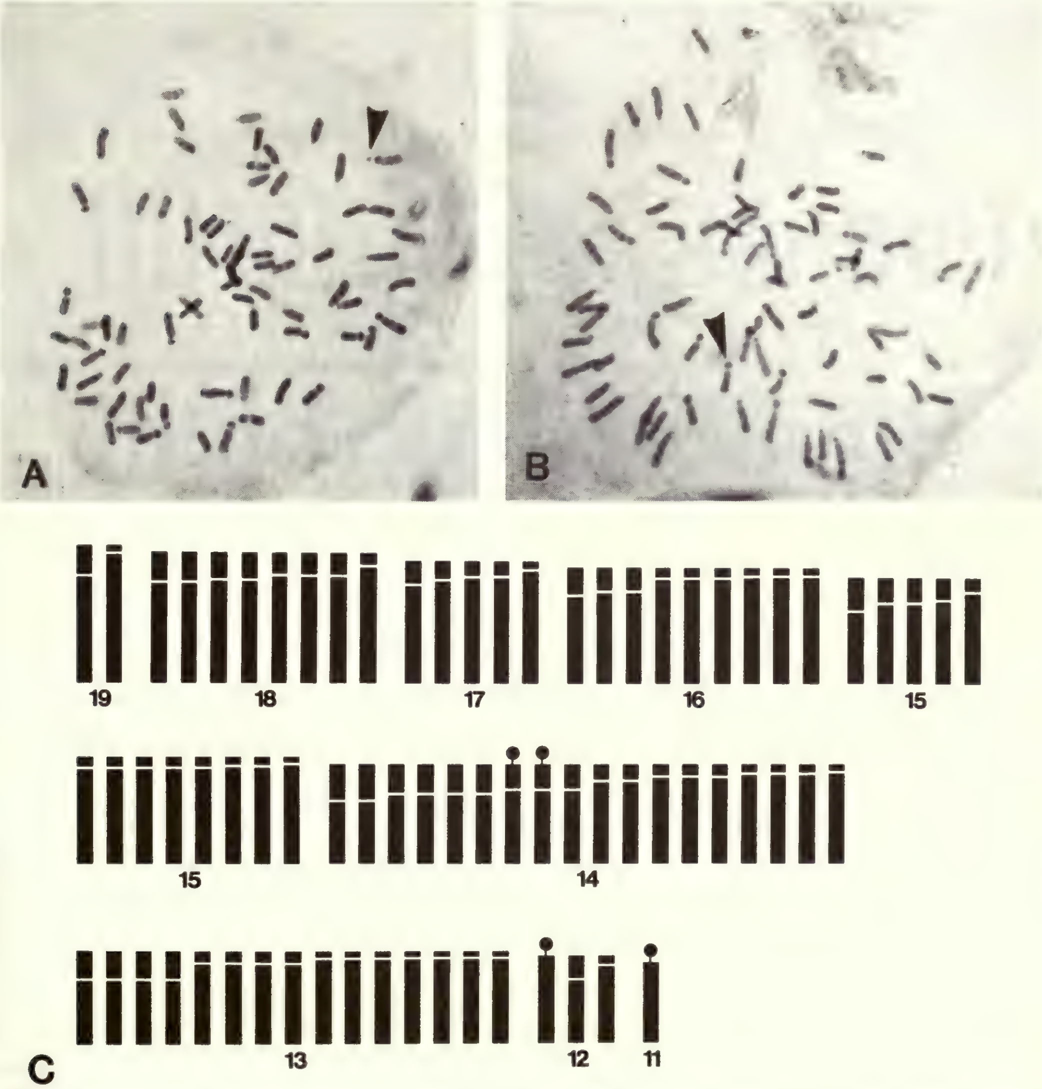

Fig. 21 *Polypodium* (subgenus *Phlebodium*). **A**, *P. loriceum*, T6486, mitosis, 2n = 74; arrow points to satellited chromosome with terminal centromere, × 1000. **B**, *P. loriceum*, T6486, mitosis, 2n = 74; arrow points to a satellited chromosome with its centromere in the subterminal (st) region, × 1000. **C**, *P. loriceum*, T6486, karyogram. Each unit of length = 0·33 μm.

P. sororium has been shown by Lellinger (1980) to be the correct name to be applied to what has almost universally been called *P. dissimile* L. He has indicated that this latter name is synonymous with, and predates that of *P. chnoodes* Sprengel, and that therefore the epithet *dissimile* must now be applied to what was *P. chnoodes*. More details of the reasons for Lellinger's nomenclatural change are given in Stolze (1981: 400–401). *P. sororium* was diploid in two localities in Trinidad with n = 37. One of the specimens was epiphytic whilst the other grew in deep humus on a stream bank.

The karyograms of *P. loriceum*, *P. triseriale*, and *P. dissimile (= P. chnoodes)* are presented in Figs 21C, 22C, & 23 respectively, together with the centromere positions in Table 14. The details of the last-named species had to be worked out on a Jamaican plant with 2n = 74 (Fig. 22B) because of the early death of a Trinidadian specimen.

Table 14 Number of chromosomes in *Polypodium* species in each centromere position (see p. 152 for explanation of symbols).

Positions	*P. loriceum* 2*x* *(Polypodium)*	*P. triseriale* 2*x* *(Polypodium)*	*P. dissimile* 2*x* *(Polypodium)*	*P. decumanum* 2*x* *(Phlebodium)*	*P. aureum* 2*x* *(Phlebodium)*	*P. aureum* 4*x* *(Phlebodium)*	*P. latum* 2*x* *(Campyloneurum)*	*P. phyllitidis* 4*x* *(Campyloneurum)*
M	0	0	0	0	0	0	0	0
m	0	4	2	2	2	0	2	0
sm	12	14	10	16	6	22	12	22
st	20 + 2*	20	10 + 2*	14	12	30	20	34
t	38	22	28	16	22	64	28	64
T	0 + 2*	12 + 2*	22	24 + 2*	30 + 2*	30 + 2*	10 + 2*	28
Total	74	74	74	74	74	148	74	148

* = additional satellited chromosomes.

Each of the three species has either two or four satellited chromosomes, but *P. loriceum* and *P. dissimile* are unique in the polypods that have been analysed in each having satellites situated on a pair of chromosomes that have their centromeres in the subterminal (st) region. This contrasts with the more normal situation whereby satellites (a pair of which is also possessed by *P. loriceum*) occur on chromosomes having their centromeres at the terminal point (T). *P. dissimile* differs from the other two species in the relatively high proportion (22 out of 74) of its chromosomes which have their centromeres at the terminal point (T).

The remaining two species are members of complexes which are poorly represented in Trinidad. One is a member of the *Polypodium pectinatum–plumula* complex, namely *P. ptilodon* var. *pilosa* which proved to be a sexual diploid with n = 37, 2n = 74. Of the other three varieties of this species recognised by Evans (1969) in his monograph of the complex he records n = 37 for var. *ptilodon* and n = 74 for var. *caespitosa* (Jenman) A. M. Evans.

The last member of this subgenus to have been examined is *P. polypodioides*, although some authors e.g. Pichi Sermolli (1977) consider this species to typify the genus *Marginaria*. Two

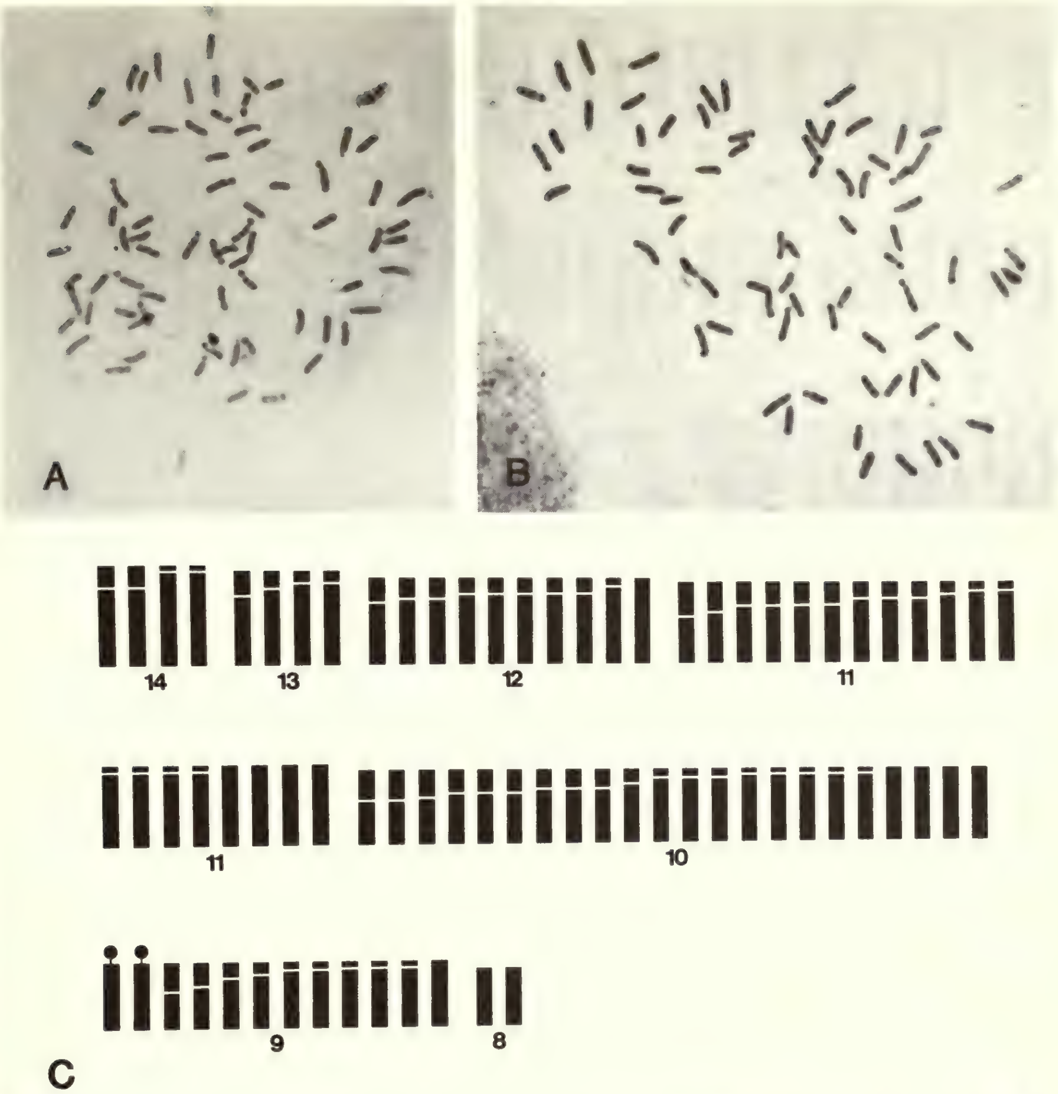

Fig. 22 *Polypodium* (subgenus *Polypodium*). **A**, *P. triseriale*, T6486, mitosis, 2n = 74, × 1000. **B**, *P. dissimile* (= *P. chnoodes*), T4566 (Jamaica), mitosis, 2n = 74, × 1000. **C**, *P. triseriale*, T6486, karyogram. Each unit of length = 0·33 μm.

levels of ploidy have been recorded for *P. polypodioides* s.l. – diploid with n = 37 from Mexico (Wagner, 1963; Evans, 1963) and from the Appalachians of U.S.A. (Wagner, Farrer & McAlpin, 1970) and tetraploid from Jamaica and Trinidad (Walker, 1966*a*). In a study of this group Weatherby (1939) distinguished the typical form of this species as being predominantly West Indian in distribution and Trinidadian material fits his description in all respects. Material from the United States and from much of Mexico on the other hand was recognised as var. *michauxianum* Weatherby. From the evidence to date it seems as if cytological and morphological differences in this species may go hand in hand, although more intensive study is necessary to confirm this.

Subgenus *Phlebodium*

All three specimens examined of *P. decumanum* were growing epiphytically – two on the trunks

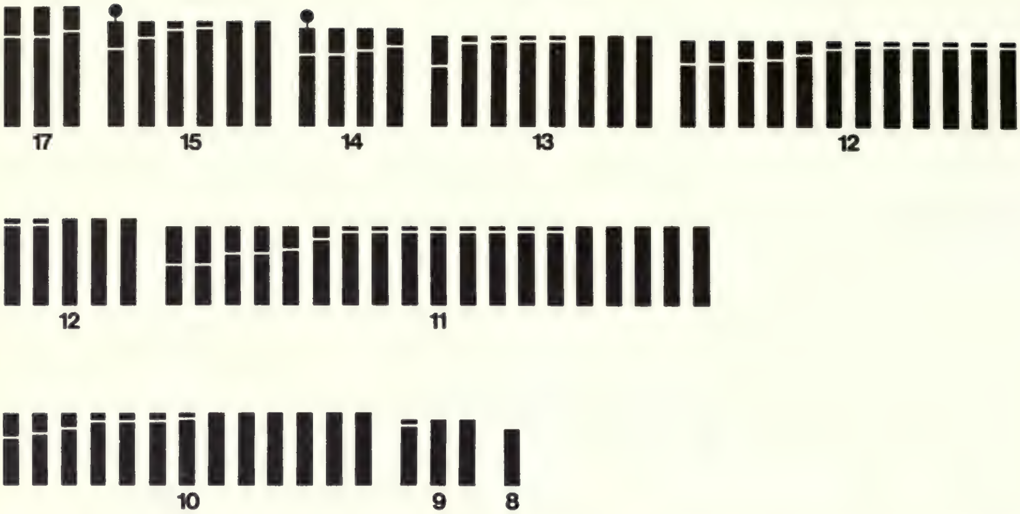

Fig. 23 *Polypodium* (subgenus *Polypodium*). *P. dissimile*, T4566, karyogram. Each unit of length = 0·33 μm.

of palms and the third on a tree branch. All were diploid with 2n = 74 (Fig. 24A & B) and their karyogram is illustrated in Fig. 24C with centromeric details in Table 14. Like the other members of *Phlebodium* considered here this species has a single pair of satellited chromosomes. These chromosomes belong to the smallest size-classes. No centromeres occur in the truly median position (M).

P. aureum s.l. is widespread in the New World, extending from Florida in the north via the tropics to subtropical regions of South America. It is popular as a house plant, especially in cases where the striking glaucous waxy bloom of the fronds is well-developed. Two major varieties have been distinguished, var. *areolatum* (Humb. & Bonpl. ex Willd.) Baker and var. *aureum*, based on whether one or two rows of sori are present and on a glaucous versus a green lamina. Diploid and tetraploid cytotypes are present but it is clear that different ploidy levels do not coincide with varietal distinctions and that the whole situation is more complicated than is usually assumed. Three plants from Jamaica (Walker, 1966*a*) were diploid with n = 37 and were clearly of the variety *areolatum*. Tetraploid plants with n = 74 were reported from Florida (Evans, 1963) and Puerto Rico (Sorsa in Fabbri, 1965; Sorsa, 1970) but without indication as to varietal status. Material from both Trinidad and Tobago is also tetraploid and sexual, forming very robust plants and agreeing with var. *aureum* in general morphology but differing in being prominently glaucous. A specimen studied from Ecuador (AAU coll. No. 3183) is similar in appearance although not so robust in growth and it proved to be diploid.

The chromosomes of the Trinidad-Tobago material of *P. aureum* clearly fall into large and small size classes at mitosis (Fig. 25A). The wide range in chromosome length may be seen in Fig. 25C and when the lengths are plotted they show a clear bimodal distribution (Fig. 26B) all of which contrasts with the small range in chromosome length and the unimodal distribution shown by diploid *P. aureum* (Figs 25B & 26A). This evidence points to the conclusion that, despite similarities between some diploid and tetraploid plants, the tetraploid did not originate by autopolyploidy, but is in fact an allopolyploid formed by hybridization between a large-chromosomed species and a small-chromosomed species followed by chromosome doubling. From the karyograms and the centromere positions (Table 14) it is somewhat doubtful whether the present form of Ecuadorian *P. aureum* could be involved in the parentage of the tetraploid.

P. aureum and *P. decumanum* have apparently spontaneously hybridized in cultivation, a plant of *P. aureum* having been displaced in the pot by the hybrid plant, which is intermediate in several respects, showing the much narrower frond shape of *P. decumanum* (Fig. 27) but having

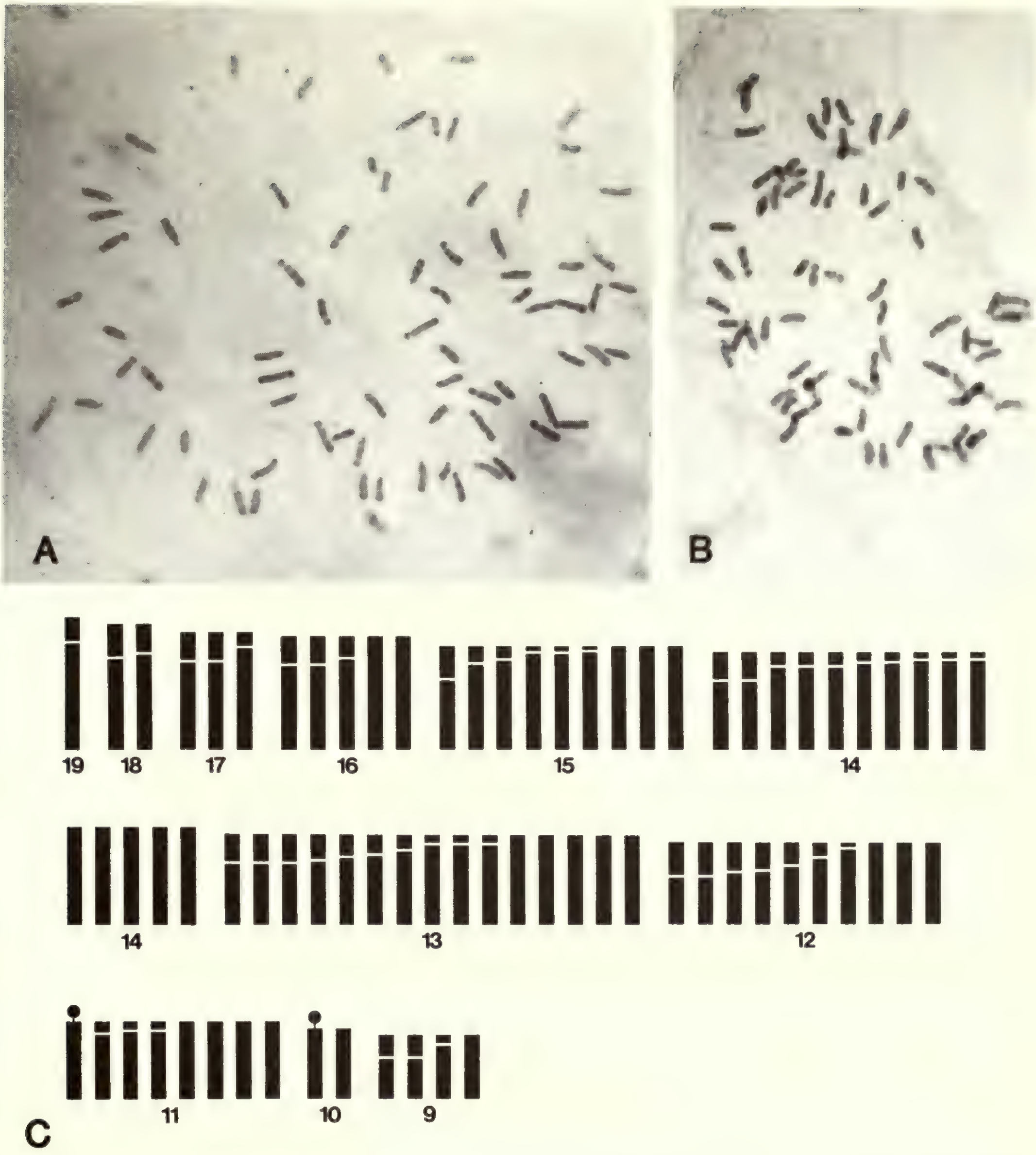

Fig. 24 *Polypodium* (subgenus *Phlebodium*) *decumanum*. **A**, T6990, mitosis, 2n = 74, × 1000. **B**, T7212, mitosis, 2n = 74, × 1000. **C**, T6990, karyogram. Each unit of length = 0·33 μm.

a small amount of the glaucous wax of *P. aureum* present, among other characters. The venation of the hybrid is that typical of *P. aureum*, with no trace of the numerous included veinlets of *P. decumanum*. Meiosis shows almost complete failure of pairing of the chromosomes, only an odd bivalent being present, suggesting no close relationship between the species (Fig. 26C & D).

An indication that *Phlebodium* is not a well-isolated genus is to be found in the fact that hybrids may be formed between members of this group and of *Polypodium* s.s. The best-known example of this is *Phlebodium* × *schneideri*, one of the classic crosses described by Schneider (1894, vol. **3**) which is a hybrid of *P. aureum* s.l. × *P. vulgare* s.l., the clone of which has persisted in cultivation to the present day.

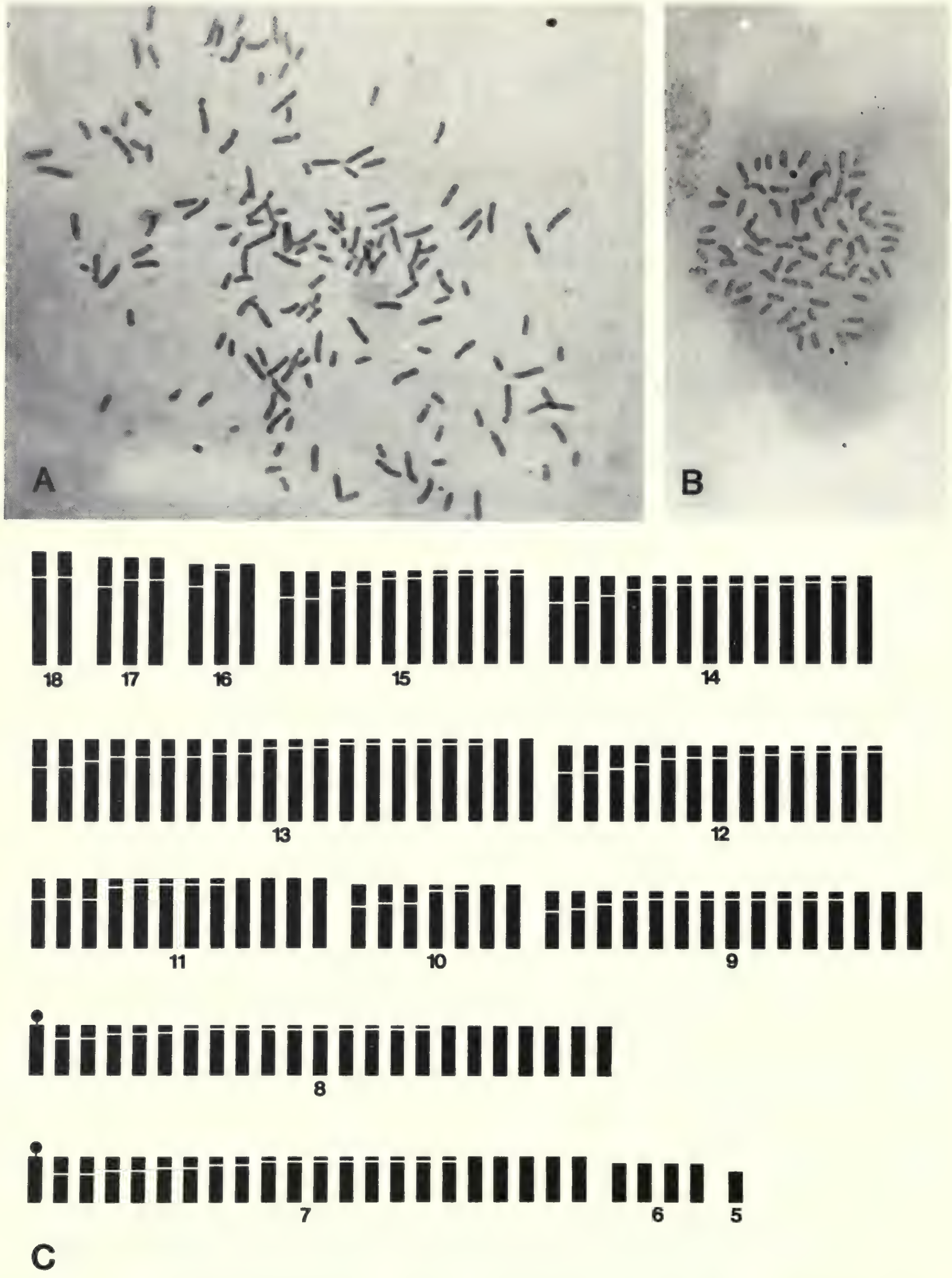
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Fig. 25 *Polypodium* (subgenus *Phlebodium*) *aureum* complex. **A**, J 11325 (4x), mitosis, 2n = 148, × 1000. **B**, AAU 3183 (2x), mitosis, 2n = 74, × 1000. **C**, karyogram of J 11325 (4x). Each unit of length = 0·33 μm.

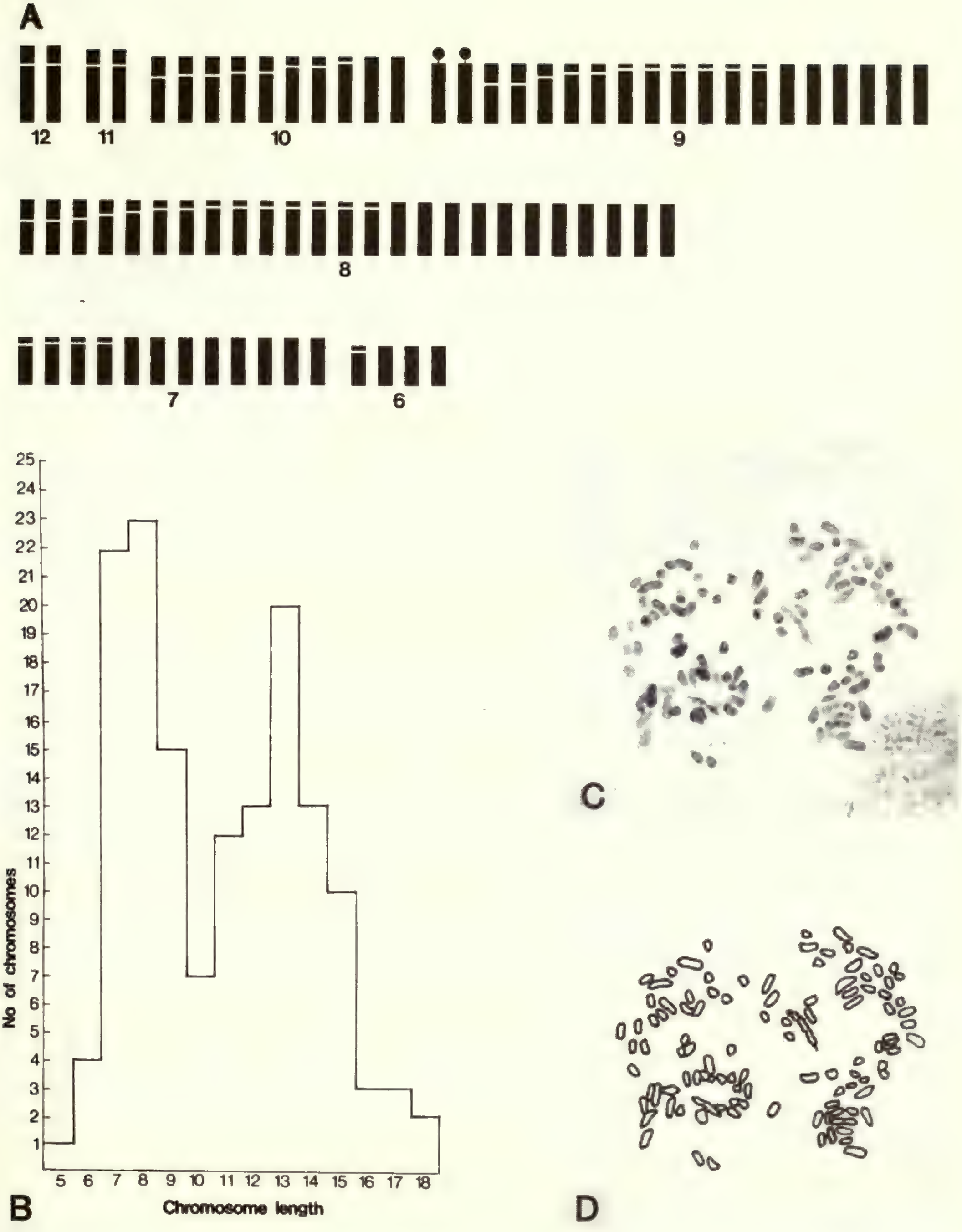

Fig. 26 *Polypodium* (subgenus *Phlebodium*). **A**, *P. aureum*, AAU 3183 (2x), karyogram, each unit of length is 0·33 μm. **B**, *P. aureum*, J 11325 (4x), histogram of chromosome lengths. **C**, putative spontaneous triploid hybrid of *P. aureum* (4x) × *P. decumanum* (2x), meiosis, × 1000. **D**, explanatory diagram of C showing 111 univalents, × 1000.

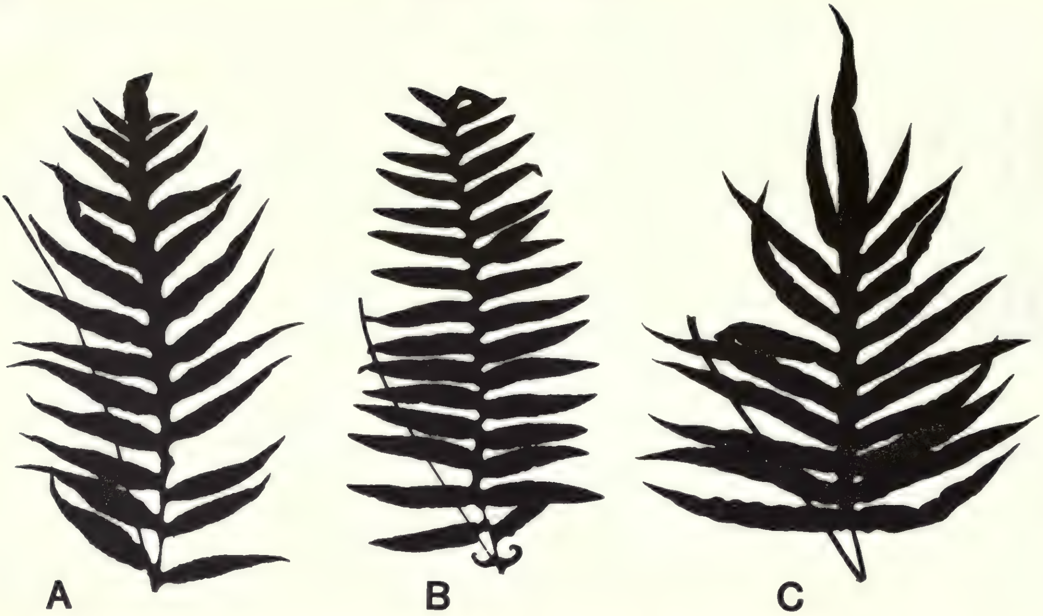

Fig. 27 *Polypodium* (subgenus *Phlebodium*). **A**, silhouette of *P. decumanum* (2x), × 1/7. **B**, silhouette of putative spontaneous triploid hybrid, *P. aureum* (4x) × *P. decumanum* (2x), × 1/7. **C**, silhouette of *P. aureum* (4x), × 1/7.

Subgenus *Campyloneurum*

P. phyllitidis and *P. latum* are common ferns in Trinidad and superficially look alike with their large simple fronds. They are, however, reasonably distinct here in the absence versus presence of stipe, the yellow-green versus dark green colour, and the flat versus undulate surface of the lamina. An additional feature which appears to have been overlooked is the presence of small hairs on the under-surface of the frond in *P. latum* and which are lacking in *P. phyllitidis*. Stolze (1981) states that he considers *P. latum* to be only a variety of *P. phyllitidis*, as in his view many of the features used to separate the two species are not always constant. However, as far as Trinidad and Tobago are concerned, they are distinct and certainly there is a sharp cytological discontinuity between them. Plants from several different localities of these two taxa show *P. latum* to be diploid and sexual with n = 37, 2n = 74, whilst *P. phyllitidis* is a sexual tetraploid with n = 74, 2n = 148. Previous reports for these species have shown *P. phyllitidis* to be also tetraploid from Florida (Evans, 1963; Wagner, 1963), Jamaica (Walker, 1966*a*, 1973*b*), and the Galapagos (Jarret, Manton & Roy, 1968), although Sorsa (in Fabbri, 1965) recorded a diploid cytotype under this name from Peru. Specimens of *P. latum* from Florida were diploid (Evans, 1963) and Smith & Mickel (1977) confirmed the diploid status of Trinidadian material on a plant collected by Dr A. Fay and subsequently grown at the New York Botanical Garden. An earlier, tetraploid count for Jamaica (Walker, 1973*a*) must be discounted due to misidentification, the specimen quoted (*Walker* T4983) actually being that of *P. repens* (Aublet) C. Presl and not *P. latum*.

Details of the somatic chromosomes of both *P. phyllitidis* and *P. latum* are shown in Figs 28A–C & 29 and Table 14. The range of chromosome length is similar in the two species and although two satellites appeared to be present in *P. latum* they could not be detected in *P. phyllitidis*. Again, it may be noted from Fig. 28C that *P. phyllitidis* shows a bimodal distribution of chromosome lengths, although not as marked as the 4x *P. aureum* implying an allopolyploid origin.

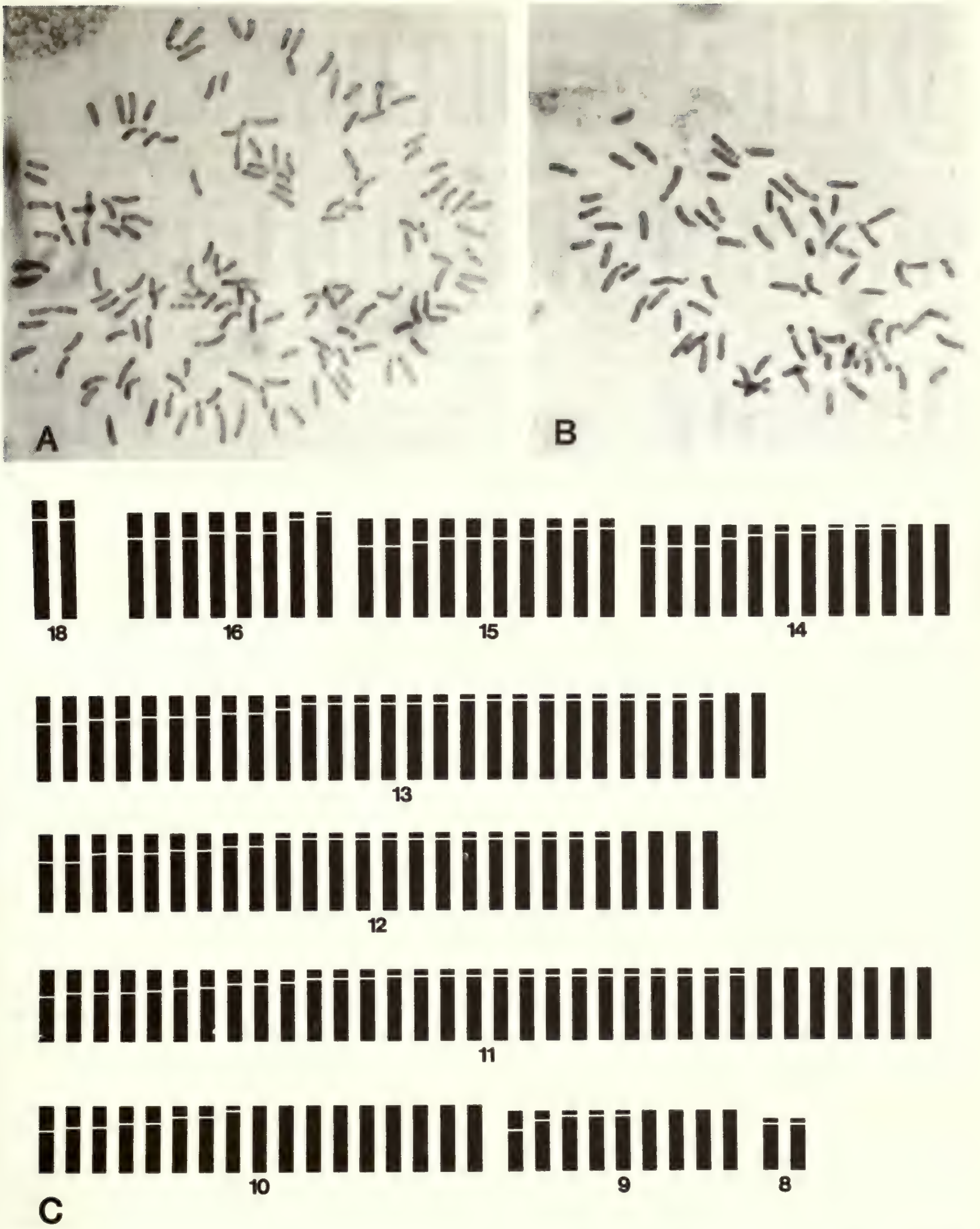
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Fig. 28 *Polypodium* (subgenus *Campyloneurum*). **A**, *P. phyllitidis*, T10986, mitosis, 2n = 148, × 1000. **B**, *P. latum*, T10605, mitosis, 2n = 74, × 1000. **C**, *P. phyllitidis*, T10986, karyogram. Each unit of length = 0·33 μm.

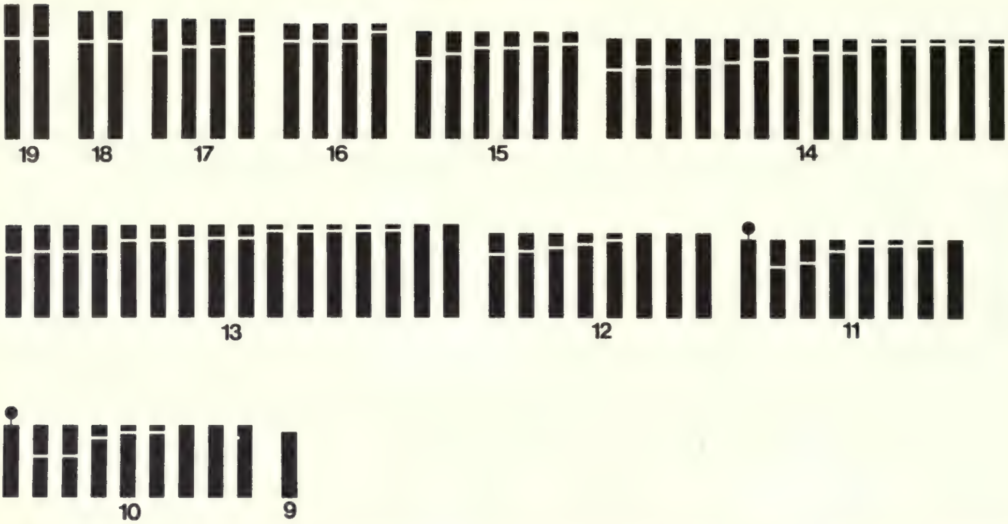

Fig. 29 *Polypodium* (subgenus *Campyloneurum*). Karyogram of *P. latum*, T10605. Each unit of length = 0·33 μm.

Subgenus *Microgramma*

Members of this group have thin, very long-creeping rhizomes, bearing at intervals small simple dimorphic fronds. The commonly occurring eiphytic *P. ciliatum* and *P. lycopodioides* are both diploid in Trinidad with n = 37. The latter species has been found to be diploid also in Jamaica (Walker, 1966*a*) and in Puerto Rico (Sorsa, 1970).

Karyotyping has not been possible in the last-mentioned genus *Microgramma*, because of lack of adequate living material. However, of the eight species which have been karyotyped, despite belonging to three different subgenera (*Campyloneurum, Phlebodium,* and *Polypodium*), all show some overall similarity in that median centromeres (either truly median at the median point M, or nearly so at the median region m) are extremely rare and range from 0% in some species up to a maximum of 5·4% in *P. triseriale.* The same is also true for the Australian *Dictymia brownii* (Wikström) Copel., another member of Polypodiaceae s.s., which has 2n = 70 and is based on x = 35 (Walker & Page, 1982). It has only four chromosomes with centromeres in the M and m positions, representing 5·7% of the total. This rarity of M and m centromeres in Polypodiaceae contrasts for example with members of Blechnaceae where M + m centromeres are much more abundant, ranging from 11·1% in *B. serrulatum* to a maximum of 22·6% in *B. occidentale.* Much more work needs to be done in this field before one can state that such differences are characteristic of families or other taxonomic groupings, but such comparisons are of great potential interest and value.

VII. GRAMMITIDACEAE

1. **Grammitis** Swartz

This generic name has been used to encompass a large group of species, numbering some 400 according to Proctor (1977) and Stolze (1981). *Grammitis* sensu lato is pantropical and has been split into a number of genera or subgenera by various authors. Despite the size of the group relatively little of the cytology is known, only some 30 species having been examined and of these more than a quarter of the chromosome numbers are quoted as approximations. Among the reasons for the lack of information is the fact that very many of the species are small and tend to grow mixed with mosses, etc., on tree trunks and frequently get overlooked. More importantly, with few exceptions they are not amenable to cultivation, nor to raising from the frequently green and very short-lived spores. Hence, as in the case of *Lindsaea*, most of the fixations have to be made in the wild, with little chance of second or more attempts if good cytological preparations are not obtained the first time. Furthermore, personal observations suggest that meiosis slows down considerably or even comes to a halt in dry periods, which are the times usually most favoured by collecting expeditions.

Despite these shortcomings it is already clear that Grammitidaceae is cytologically diverse, with base numbers of x = 32, 33, 35, 36, and 37 having been reported definitely and substantiated by good photographic evidence. Experience suggests that this aneuploid series will be extended as more results become available. Both the differing opinions regarding possible generic limits and the cytological diversity already revealed in the small percentage of the family which has been sampled help to confirm that a thorough monographic treatment on a world-wide basis is needed.

Löve, Löve & Pichi Sermolli (1977) quote results for a number of species of *Grammitis* under the generic name of *Xiphopteris*, with accurate determinations of x = 37 quoted for *X. cornigera* (Baker) Copel. by Manton & Sledge (1954), and for *X. myosuroides* (Swartz) Kaulf. by Walker (1966*a*); and x = 33 in *X. hartii* (Jenman) Copel. (Walker, 1966*a*) as well as several other approximate counts. F. S. Wagner (1980) has determined *X. limula* Christ as having n = 32.

Grammitis taenifolia is one of the more conspicuous members of the genus with its deeply pinnatifid fronds which closely approach in general appearance those found in many members of *Polypodiaceae* s.s. This species has been placed in the genus *Xiphopteris* (see below), but I prefer to consider it here as a member of *Grammitis*. Tapetal mitotic nuclei showed 2n = 74 fairly clearly (Fig. 30A & B) and the species is therefore a diploid based on x = 37, a commonly occurring number in the family (see Löve, Löve & Pichi Sermolli, 1977, for references).

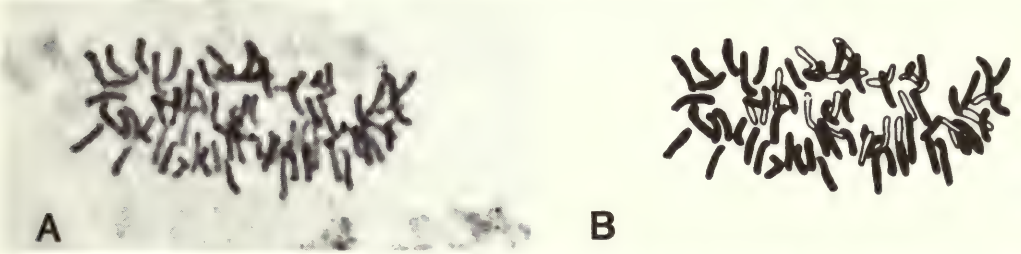

Fig. 30 *Grammitis taenifolia.* **A**, T6811, tapetal mitosis, 2n = 74, × 1000. **B**, explanatory diagram, × 1000.

2. Cochlidium Kaulf.

This genus, bearing coenosori along the midrib has been associated in the past with the vittarioid ferns. Christensen (1929) in a detailed study showed that this association was not soundly based and that the genus was polypodioid in the broad sense, and *Cochlidium* is considered today as a member of the Grammitidaceae.

F. S. Wagner (1980) published a very elegant photograph demonstrating n = 33 in a plant of *C. rostratum* (Hook.) Maxon ex C.Chr. from Costa Rica. The sole Trinidadian representative examined belonging to this genus, *C.* aff. *linearifolium*, gave rather poor quality preparations in which the chromosome number was determined as being n = 33 or 34, there being doubt at one point in particular where a bivalent had despiralized, obscuring details of the outline of nearby members. However, the number is in general agreement with that reported by Wagner in *C. rostratum*.

This Trinidad plant requires further investigation in that its characters do not fit in a number of details with those of *C. linearifolium* as enumerated by Bishop (1978). Some of the characters are those of *C. rostratum*, but again there is not complete accord. Meiosis in the specimen examined is regular and there is no suggestion that the plant may be a hybrid between these two species.

3. **Xiphopteris** Kaulf.

In his revision of *Cochlidium*, Bishop (1978) included *Xiphopteris serrulata* as one of the 16 species he recognised as belonging to the same genus, pointing out that its characters are at variance with some members of *Xiphopteris* of which it was the type species. However, Bishop draws attention to the ways in which it also differs from the other species of *Cochlidium* and, although preferring to include *X. serrulata* within *Cochlidium*, he acknowledges that in view of its distinctness it might reasonably be retained in its own monotypic genus. Until a full investigation of the group is completed, I prefer to consider *X. serrulata* the sole member of the genus.

Previous chromosome counts for this widespread species have been recorded as n = *c.* 74 bivalents, whilst most cells showed *c.* 148 univalents (Walker, 1966*a*) in Jamaican specimens, whilst Araujo (1976) quoted n = 74 for Brazilian material, all these being tentatively based on x = 37, although Jamaican counts were quoted as approximations only. However, Trinidadian plants gave clear preparations in which 105 univalents were clearly present (Fig. 31A & B) and several cells gave the same result. This seemingly anomalous result caused me to thoroughly search again through my permanent Jamaican preparations and a hitherto unrecorded plant of *X. serrulata* (T5077 from Lawrence Bottom, Portland), also showed 105 univalents (Fig. 31C & D). Some better cells were discovered on a slide of plant number T1733, originally quoted as having approximately 148 univalents. These cells showed 140 univalents (Fig. 31E & F). Thus in Jamaica there are plants with 105 and 140 univalents which represent the triploid and tetraploid

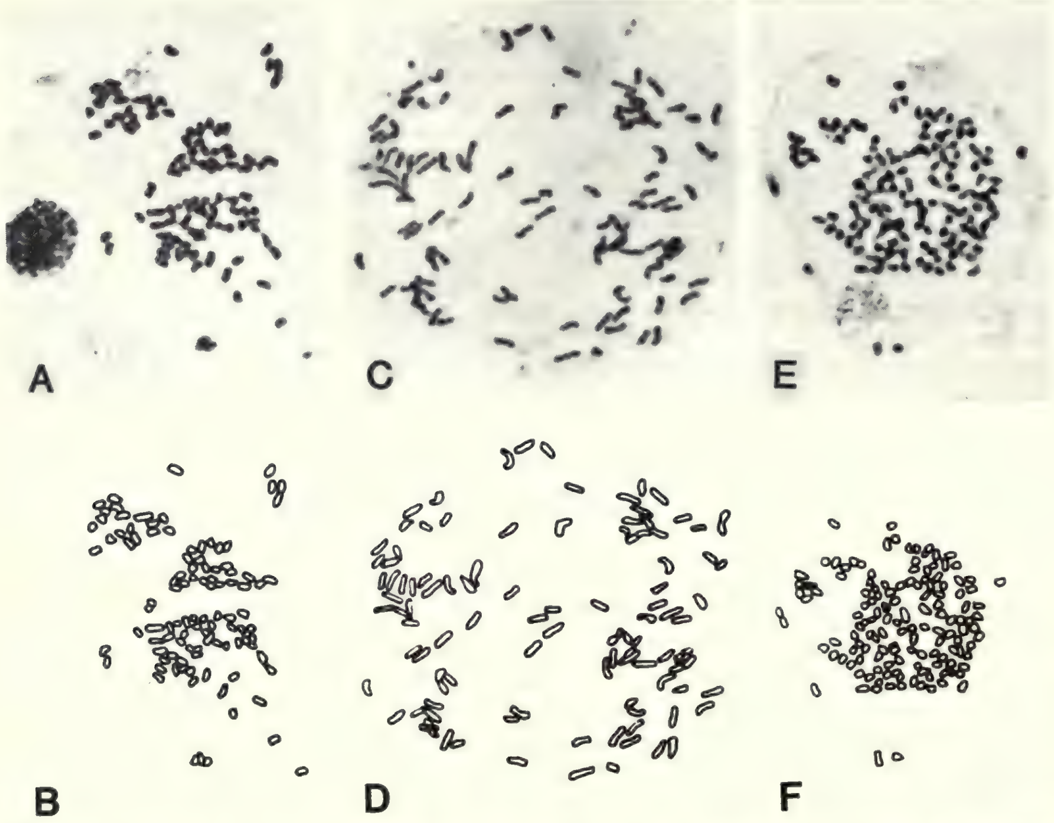

Fig. 31 *Xiphopteris serrulata*. **A**, T10976 (Trinidad; 3x), 'n' = 105, × 1000. **B**, explanatory diagram of A, 105 univalents, × 1000. **C**, T5077 (Jamaica; 3x), 'n' = 105, × 1000. **D**, explanatory diagram of C, 105 univalents, × 1000. **E**, T1733 (Jamaica; 4x), 'n' = 140, × 1000. **F**, explanatory diagram of E, 140 univalents, × 1000.

levels of a polyploid series based on x = 35 (and not 37 as hitherto assumed). In Trinidad the triploid is present, although further sampling may show other levels as well. A morphological comparison of the triploids and tetraploids was not very rewarding, the plants being so similar (and simple) in structure. However, there appeared to be a tendency for the triploids to be more slender and thinner in texture than the tetraploid and with more conspicuous veins. On the other hand stomatal length proved to be a good distinguishing feature with no overlap in the measurements, the mean for both the Jamaican and Trinidadian triploids being 52·0 μm (from 45·0 to 60·0 μm), whilst the mean of the tetraploid was 68·0 μm (from 64·0 to 79·0 μm).

The presence of numerous cells with univalents only in both Trinidadian and Jamaican material suggests that these are agamosporous cytotypes following the Braithwaite system of sporogenesis. It may also be noted especially in Fig. 31C that the univalents vary appreciably in size within a cell.

VIII. CYATHEACEAE

In his treatment of the tree ferns for *Flora malesiana* Holttum (1963) published a conspectus of the family setting out his views on affinities within the group. These views also took into account anatomical (Holttum & Sen, 1961) and cytological evidence in addition to morphological characters. More recently Holttum (Holttum & Tryon, 1977) has modified his views somewhat in so far as he now believes that the four subfamilies he recognised as constituting Cyatheaceae embraced too broad a concept and that each should be raised to family rank. As presently construed Cyatheaceae sensu Holttum would include *Dicksonia* and *Cystodium* in addition to the monotypic *Lophosoria*, a small American genus *Cnemidaria*, and the huge genus *Cyathea* which comprises overwhelmingly the vast majority of the tree ferns. This latter genus was subdivided into two subgenera – *Cyathea* and *Sphaeropteris* – on the basis of characters of the stipe scales. Each subgenus was further split into sections and in the case of *Sphaeropteris* into subsections as well.

Parallel attention was given by Tryon (1970) to the tree ferns with particular, but not exclusive, reference to those of the New World. Apart from the inclusion of the two monotypic genera *Lophosoria* and *Metaxya*, all the other members of his Cyatheaceae would have been subsumed under Holttum's *Cnemidaria* and *Cyathea*. Tryon ascribed these members to six genera, namely *Alsophila, Cnemidaria, Cyathea, Nephelea, Sphaeropteris,* and *Trichipteris*, in which the development and mature structure of the scales played an important role as in Holttum's scheme. Tryon's original outline has now been amplified by monographic treatment of each of his genera, viz. *Cnemidaria* (Stolze, 1974), *Cyathea* (Tryon, 1976), *Nephelea* (Gastony, 1973), *Sphaeropteris* (Windisch, 1977), *Trichipteris* (Barrington, 1978), *Alsophila* (outline by Tryon & Tryon, 1982). A number of other papers deal with more specialized aspects such as anatomy, ontogeny, biogeography, and spore morphology – references to which will be found in Holttum & Tryon (1977).

Although both *Lophosoria* and *Metaxya* occur in Trinidad they were not obtained in a fixable condition and no further discussion will be entered into regarding their possible inclusion or otherwise in Cyatheaceae. Of the six species of Trinidadian tree ferns (*Cyathea* s.l.) which have been looked at cytologically *C. tenera* would be assigned by Tryon to *Cyathea* s.s.; *C. hirsuta* to *Sphaeropteris*; *C. aspera*, *C. microdonta*, and *C. sagittifolia* to *Trichipteris*; and *C. spectabilis* to *Cnemidaria*. The synonymy is given in the list of chromosome numbers in Table 2.

All of these Trinidadian species are exceedingly uniform cytologically, having n = 69, and all represent new specific records except for *C. microdonta* which likewise had n = 69 in Jamaican material (Walker, 1966*a*). This cytological uniformity is common throughout *Cyathea* s.l. of which approximately 40 species have been examined from many parts of the world (for literature references see Löve, Löve & Pichi Sermolli, 1977). Only four possible exceptions to n = 69 have been reported of which the three following species had their chromosome numbers reported as approximations (and which therefore in fact may not be exceptions); *C. camerooniana* Hook. (Manton 1959), *C. hookeri* Thwaites (Manton & Sledge, 1954; Abraham, Ninan & Mathew, 1962), and *C. sinuata* Hook. (Manton & Sledge, 1954; Abraham, Ninan & Mathew, 1962). The only positive assertion of a number differing from 69 is that for *C. capensis* (L.f.) J.Smith with n = 70 by Manton & Sledge (1954) and by Abraham, Ninan & Mathew (1962).

The genus *Cyathea* s.l. is a very large one with the number of species in excess of 600, divided more or less equally between the two hemispheres. Unlike most other large groups of ferns the chromosome number is very stable as has been indicated, even extending to the absence of polyploidy in the genus as far as is known. Nevertheless, it is clear from its high basic chromosome number seen today that the group undoubtedly had a polyploid origin in the geological past, and that at the present day evolution is by genetic means rather than by the changes in chromosome numbers, which are such a common feature in many other ferns. Such a large genus is not easy to handle conveniently from the taxonomic viewpoint, but the evidence points to it being monophyletic. Despite the recognition of six genera by Tryon, evidence published by himself and his students strongly indicates that these do not rank as full genera in the biological sense in that they are not genetically isolated from one another. Indeed, Tryon (1970) and Conant (1975) between them list 14 different 'intergeneric' hybrids involving *Cnemidaria* × *Cyathea* (3 different combinations), *Cnemidaria* × *Trichipteris* (1), *Cyathea* × *Trichipteris* (5), and *Alsophila* × *Nephelea* (5). In the case of the last group, Conant (1975) produces convincing evidence that not only are hybrids produced between *Alsophila dryopteroides* (Maxon) Tryon and *Nephelea portoricensis* (Kuhn) Tryon in Puerto Rico, but that well-developed spores are formed. *Alsophila bryophila* Tryon has also been shown by Conant & Cooper-Driver (1980) to hybridize with these two species, producing a fertile hybrid swarm resulting in F_2 segregates of which some are stable and resemble other species. Gene-flow on such a scale, at least in the ferns, is hardly consistent with generic separation and if the six groups have validity at all they are probably better regarded as subgenera of *Cyathea*.

IX. DENNSTAEDTIACEAE

1. **Dennstaedtia** Bernh.

Dennstaedtia is the central member of the family Dennstaedtiaceae which has long been recognized as occupying a key phylogenetic position. Nevertheless it is still in a confused state taxonomically and in need of monographic study on a world-wide basis as has been pointed out in particular by Holttum (1973) and Mickel (1973). Within the genus as at present defined the cytological situation is complex, showing a range of base numbers which have a bimodal distribution, these being x = 30, 31, 32, 33, 34 and 46, 47. Both Walker (1973*a*) and Lovis (1977) have discussed the implications of this in some detail and the reader is referred to these papers for further information.

In Trinidad, however, the situation is simple in that according to Tryon (1960) only three of the 11 species recorded for the Americas are present, namely *D. bipinnata, D. dissecta* (Swartz) T. Moore and *D. obtusifolia.* Of these, the first and last have been cytologically examined from the island.

D. bipinnata is tetraploid in Trinidad with n = *c.* 94, 2n = *c.* 188, the preparations not being of sufficiently high quality to determine whether this species is founded on a basic number of x = 46 or 47. However, the level of ploidy is the same as that recorded for Jamaica as n = 94 by Walker (1966*a*).

D. obtusifolia is diploid, showing n = 46 very clearly (Fig. 32). This number has also been found to occur in Mexican *D. dissecta* by Mickel, Wagner & Chen (1966), although later Smith & Mickel (1977) stated that it was n = 47, and noted this was in conflict with the earlier report. *D. obtusifolia* is also diploid in Puerto Rico according to Sorsa (1970) who gave the approximation n = *c.* 47.

2. **Pteridium** Gled. ex Scop.

Bracken (*Pteridium aquilinum*) was examined from a locality in the hills overlooking Port of Spain. The area was a few hectares in extent, fully exposed to the sun and had been recently burnt over. The plant belonged to the variety *arachnoideum* and gave a somatic chromosome

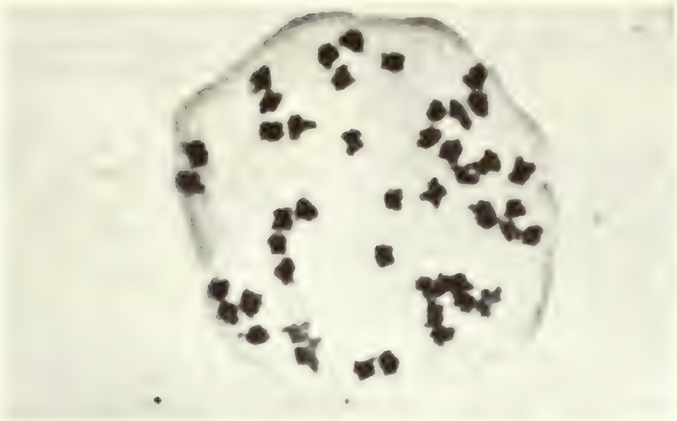

Fig. 32 *Dennstaedtia obtusifolia,* T10600, meiosis, n = 46, × 1000.

count of 2n = 104 (Walker, quoted in Page, 1976). Since Löve and Kjellquist have shown that a population of *P. aquilinum* s.l. from S. Spain now known as *P. herediae* (Clemente ex Colmeiro) Löve & Kjellqvist to have 2n = 52 (Molesworth-Allen, 1968), the basic chromosome number of this genus, which had previously been accepted as x = 52, has had to be revised to x = 26. The Trinidadian specimen of bracken is thus tetraploid. Two other specimens of var. *arachnoideum* have been examined elsewhere, both from the Galapagos Islands, one also being tetraploid with n = 52, the other being octoploid with 2n = 208 and an irregular meiosis (Jarrett, Manton & Roy, 1968).

3. **Lindsaea** Dryander ex Smith

Only six or seven species of *Lindsaea* occur in Trinidad, a particularly surprising fact when one considers the relative closeness of the island to the big centre of speciation, namely the Guiana-Shield which has 33 species, of which 14 are endemic (Kramer, 1957). The isolation of Trinidad in this respect is made even more curious by the physical continuity of the island with the land mass of South America in comparatively recent times. Indeed *Lindsaea* itself is the only representative of the subfamily Lindsaeoideae, although *Odontosoria, Ormoloma,* and *Sphenomeris* occur elsewhere in the West Indies.

Reports of chromosome numbers for New World species of *Lindsaea* are few in number. *L. arcuata* Kunze from Mexico was reported as having n = *c.* 84 (Mickel, Wagner & Chen, 1966) and n = *c.* 88 (Smith & Mickel, 1977), whilst Tryon, Bautista & Araujo (1975) reported counts for four taxa from Brazil, namely *L. divaricata* Klotzsch with n = 42, *L. schomburgkii* Klotzsch with n = *c.* 84, *L. quadrangularis* ssp. *subulata* Kramer, showing *c.* 84–88 chromosomes, mainly as univalents and *L. lancea* var. *falcata* (Dryand.) Rosenst. with n = 42. My own specimen of this latter variety was obtained on the wet edges of wallow holes in Long Stretch Forest Reserve and gave poor preparations in which the chromosome number could not be determined with accuracy but which lay between the limits of n = 41–44. This is therefore at the same diploid level of ploidy as the Brazilian plant reported by Tryon et al.

Two varieties of *L. stricta* have been cytologically examined from Trinidad, namely var. *stricta* (found on roadside cuttings) and var. *parvula* (Fig. 33A & B) from the edge of drainage channels on Aripo Savanna. Both were tetraploids, showing *c.* 88 pairs of chromosomes at meiosis. This figure represents the upper limit and the precise number may be somewhat less than this.

Two specimens of *L. portoricensis* from different habitats were examined. One was growing at the edge of a wallow hole in Long Stretch Forest Reserve in sandy soil, whilst the other was on a steep clay roadside cutting in Aripo Valley. Both proved to be tetraploids with n = *c.* 88 as was also the case for this species in Jamaica (Walker, 1966*a*), the representative counted coming from boggy ground.

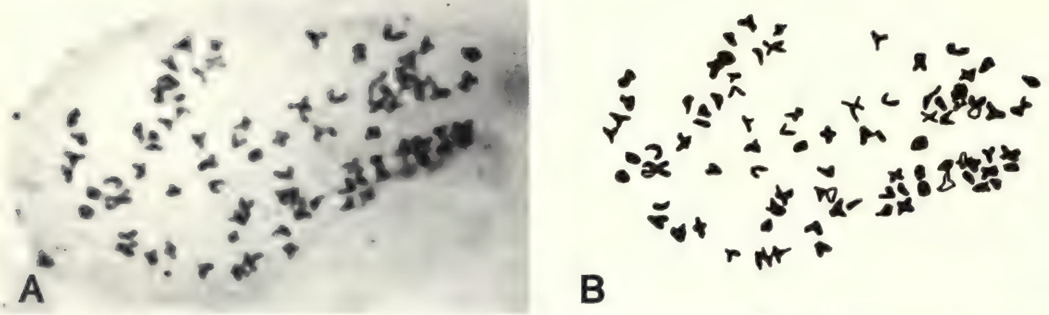

Fig. 33 *Lindsaea stricta* var. *parvula*, T6368. **A**, meiosis, n = 88, × 1000. **B**, explanatory diagram, all bivalents, × 1000.

Although it is clear that there is indeed an aneuploid series of basic chromosome number in *Lindsaea* (x = 34, *c.* 40, 42, 44, 47, *c.* 50), one of the striking features of the cytology of this genus is the number of counts obtained which are only approximate and hence it has so far not been possible to determine whether particular base numbers are associated with the various subgenera and sections in Kramer's monograph (1957). The reasons for this lack of accuracy have been discussed in more detail elsewhere (Walker, 1973*a*; Lovis, 1977), suffice it to say that few meioting sporangia are available at any one time in fixations made in the field, although biologically it may have the advantage that spore production in individual fronds is evenly spread over a long time. A further hazard for the cytologist is that the plants are not very amenable to cultivation, hence if a fixing is not successful in the field it is not usually possible to repeat it in the greenhouse. Even Schneider (1893) who raised so many fern genera with success admitted that it was a difficult group, and commented that most living plants of *Lindsaea* ended up as herbarium specimens!

X. THELYPTERIDACEAE

In order to provide a workable basis for discussion in the cytological survey of the Jamaican ferns (Walker, 1966*a*, 1973*b*), the species of this family were considered under the appropriate subgenera proposed by Christensen (1913, 1920) in his monograph of the tropical American species of *Dryopteris* sensu latissimo. This scheme of grouping the thelypterids was adopted in principle by Morton (1963) with the appropriate nomenclatural changes. Since this time intensive study of Thelypteridaceae of the Old World led Holttum (1971) to produce a scheme in which he recognised 23 genera, most of which have now been individually monographed by him. It is noteworthy that although the family shows an aneuploid range of chromosome numbers from 27 to 36, each of Holttum's genera is uniform in having a single base number, although of course several genera may have the same number in common, thus slightly more than half the genera are based on x = 36. Similarly, SEM studies of spore morphology (Wood, 1973) have shown a close correlation with chromosome number in many of the taxa.

Whilst work on the New World members of the family has not yet resulted in a comparable scheme, nevertheless a substantial number of the species that have been examined from Trinidad belong to genera which are represented in the Old World and are consequently disposed according to Holttum's scheme. Furthermore, the group of species corresponding in large part of Christensen's subgenus *Lastrea* and which are almost wholly American in origin, are very uniform cytologically, having the very unusual number in Thelypteridaceae of x = 29 (Walker, 1966*a*, 1973*b*; Smith, 1971*a*, 1973; Smith & Mickel, 1977; Sorsa in Fabbri, 1965). In addition the spores have a very distinctive raised reticulation (Wood, 1973; Holttum, 1975) and lack a perispore wing. This group has been closely studied by Smith (1973) who treats it as subgenus *Amauropelta* of *Thelypteris*. It can equally be recognised at generic rank and this is the course adopted here. This leaves two groups of thelypterids remaining, namely *Goniopteris* and

Meniscium, which await further study and which are possibly not homogenous. However, I have retained the names for convenience and consistency whilst recognising that these two groups may need extensive revision in the light of future work.

1. **Amauropelta** Kunze

This genus corresponds to the subgenus *Lastrea* in Christensen (1913, 1920) and is a large assemblage of some 200 species, occurring, with few exceptions, exclusively in the tropical and subtropical regions of the New World. Smith (1974), although treating it as a subgenus of *Thelypteris*, considers the group to be a natural one and probably monophyletic. He has subdivided *Amauropelta* into nine sections. Cytological data are available from a variety of sources, in particular Jamaica and Mexico, of representatives of each of the sections, and the highly distinctive base number of $x = 29$ is universally present. This cytological constancy is also reflected in the characteristic spore patterning described by Wood (1973).

The genus is poorly represented in Trinidad and only two species were cytologically examined, these being *A. oligocarpa* and *A. opposita*. The former is the type species of Smith's section *Uncinella*, comprising some 50 species. *A. oligocarpa* is diploid with $n = 29$, the same as has been reported for this species from Jamaica (Walker, 1966*a*) and Mexico (Smith, 1971*a*). All the other members of the section which have been counted are also diploid, these being *A. diplazioides* (Desv.) Pichi-Serm. from Jamaica (Walker, 1966*a*), *A. heteroclita* (Desv.) Pichi-Serm. also from Jamaica (Walker, 1966*a*), *A. linkiana* (C. Presl) A. Löve & D. Löve from Mexico (Smith, 1971*a*), and *A. navarrensis* (Christ) Pichi-Serm. from Costa Rica (Smith, 1971*a*).

A. opposita is a member of section *Amauropelta* which again consists of some 50 species. The centre of evolution lies in the West Indies where approximately 40% are endemic to one or a few islands (Smith, 1974). Two specimens, one from Trinidad and the other from Tobago, were diploid with $n = 58$. Other members of this section for which there is cytological information are *A. nockiana* (Jenman) Pichi-Serm. from Jamaica (Walker, 1966*a*), *A. sancta* (L.) Pichi-Serm. from Jamaica (Walker, 1966*a*, 1973*b*), *A. sanctiformis* (C.Chr.) A. Löve & D. Löve from Mexico (Smith, 1973), and A. aff. *underwoodiana* from Jamaica (Walker, 1973*b*), all again being diploids with $n = 29$. Some confusion exists regarding *A. resinifera* (Desv.) Pichi-Serm. This was reported as having $n = 29$ from Mexico (Smith, 1971*a*). Earlier reports were of $n = 31$ by Mickel, Wagner & Chen (1966) and $n = c.\ 62$, $2n = c.\ 124$ from Jamaica (Walker, 1966*a*). The latter were poor preparations which gave only approximate counts and they probably represent the tetraploid level based on actual numbers of $n = 58$ and $2n = 116$. Nevertheless it is clear that in this species both diploid and tetraploid levels occur.

2. **Macrothelypteris** (H. Itô) Ching

M. torresiana is another thelypterid fern whose natural habitat is tropical Asia and the Pacific, but which has become naturalized in the New World, ranging from Florida and the Caribbean to South America. This species is very distinctive, not only by virtue of its glaucous stipe, but by the highly characteristic pungent smell that living plants possess.

Tetraploids (based on $x = 31$) showing 62 pairs of chromosomes at meiosis have been reported from Singapore (Manton in Holttum, 1954), India (Loyal, 1961; Abraham, Ninan & Matthew, 1962; Ghatak, 1962), and Sri Lanka (Manton in Holttum, 1954). In addition to the tetraploid Manton also demonstrated the presence of a hexaploid with $n = 93$ in Sri Lanka. In the New World the only previous record, under the name *Thelypteris uliginosa* (Kunze) Ching, has been at the tetraploid level from Jamaica, the same as has now been established for Trinidadian material.

3. **Goniopteris** C. Presl

Goniopteris is an American genus of upward of 70 species, characteristically bearing forked or stellate hairs and with a basic chromosome number of $x = 36$. Some 24 taxa have been cytologically examined and diploids and tetraploids are present in more or less equal numbers. A further two new records for the genus are provided by Trinidadian material, namely the bulbil-bearing *G. paucijuga* which is diploid with 2n = 72 and *G. nephrodioides*, a tetraploid with n = 72.

G. pennata, better known as *G. megalodus* (Schkuhr) C. Presl is diploid in both Jamaica (Walker, 1966*a*, 1973*b*) and in Trinidad. By contrast Kurita (1963) reported this species as having n = 72 but this was determined on botanic garden material of unknown provenance. However, it does suggest that there may be a small complex centred on this species.

G. poiteana is cytologically known from a number of countries viz. Trinidad, Tobago, Jamaica (Walker, 1966*a*, 1973*b*), Mexico (Smith & Mickel, 1977) and Galapagos (Jarrett, Manton & Roy, 1968) and has proved to be uniformly tetraploid. By contrast the similarly widely-distributed *G. tetragona* is cytologically variable, being tetraploid in Trinidad, Tobago, Jamaica (Walker, 1966*a*, 1973*b*) and Florida (Smith, 1971*a*) whilst both diploid and tetraploid forms have been reported from Mexico (Mickel, Wagner & Chen, 1966; Smith, 1971*a*; Smith & Mickel, 1977). This species is also morphologically very variable with several forms being intermediate with other species (Christensen, 1913).

Three plants were collected which were superficially very similar to *G. paucijuga* but which did not agree with the specific description in detail. They proved to be triploid with *c.* 108 chromosomes associated as univalents and bivalents at meiosis and giving rise to spores which were very irregular in size and shape. A comparison of features (Table 15) suggests that these are hybrids between the diploid *G. paucijuga* (Fig. 34A & B) and the tetraploid *G. tetragona* (Fig. 34E & F) and are called *G.* × *tabaquitensis* (Fig. 34C & D) (Jermy & Walker, 1985).

That *Goniopteris* is a genus in a state of active evolution which would well repay monographic study is suggested by a number of species that have both diploid and tetraploid cytotypes, the wide range of morphological variation within and between species, and in the formation of hybrids linking different taxa.

Table 15 Comparison of *Goniopteris paucijuga, G. tetragona,* and their hybrid *G.* × *tabaquitensis.*

Character	*G. paucijuga*	*G.* × *tabaquitensis*	*G. tetragona*
1. Frond apex	apex pinnatifid	apex pinnatifid	terminal pinna
2. Pinnae	sessile, strongly reflexed	shortly stalked, strongly reflexed	stalked, variably reflexed
3. Hairs:			
a) frond adaxial surface	absent	present on margins, costae and costules	few simple hairs on lamina present on veins, costules, costae and margins
b) frond abaxial surface	very sparse on costae, absent elsewhere	very sparse on all parts, more conspicuous on costae	sparse on lamina and veins conspicuous on costules, very conspicuous on costae (mixture of long and short hairs)
4. Proliferous buds	present in axils of upper pinnae	present in axils of upper pinnae	absent
5. Indusium	hairy	hairy	absent
6. Sporangia	sporangial capsule glabrous, stalk with single conspicuous hair	sporangial capsule glabrous, stalk for most part glabrous	sporangial capsule setulose, stalk glabrous
7. Cytology	diploid	triploid	tetraploid

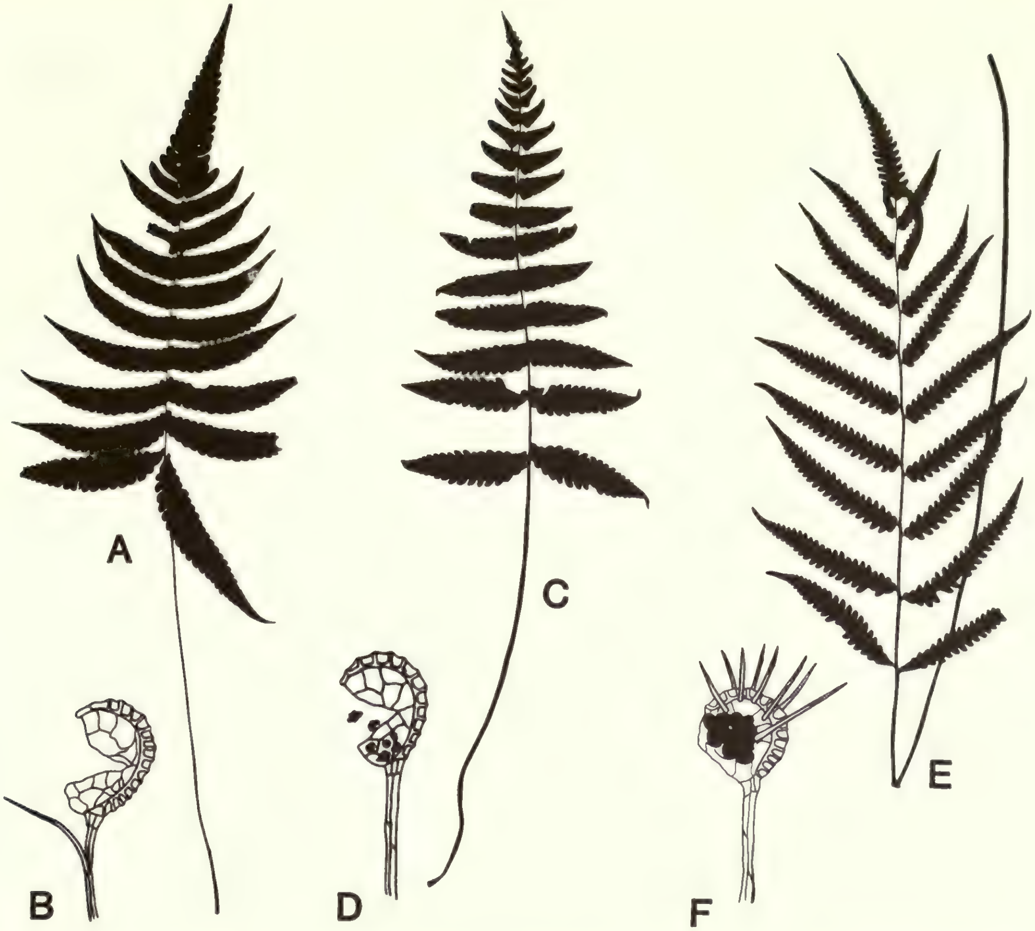

Fig. 34 *Goniopteris*. **A**, *G. paucijuga*, T7056 (2x), silhouette, × 1/4. **B**, *G. paucijuga*, sporangium × 50. **C**, *G.* × *tabaquitensis*, T6194 (3x), silhouette, × 1/4. **D**, *G.* × *tabaquitensis*, sporangium, × 50. **E**, *G. tetragona*, T7206 (4x), silhouette, × 1/4. **F**, *G. tetragona*, sporangium, × 50.

4. **Meniscium** Schreber

Cytological records exist for only three species of this small American genus, namely *M. nesioticum, M. reticulatum* (L.) Swartz, and *M. serratum*. These species have creeping rhizomes and show rather weak dimorphism, although this is rather more pronounced in the case of *M. reticulatum*.

M. serratum has been investigated from three localities in Trinidad, nearly all the plants growing in boggy situations. It is a sexual diploid (n = 36, 2n = 72) as has been found to be the case in Florida (Wagner, 1963).

M. nesioticum, often confused with the larger *M. reticulatum*, is tetraploid with n = 72 in Trinidad, as is the latter in Puerto Rico (Sorsa in Fabbri, 1965; Sorsa, 1970) and Jamaica (Walker, 1966*a*). In *M. nesioticum* the very young exindusiate sori are conspicuously reddish-purple – a feature which to some extent is retained in herbarium specimens. The annuli of young sporangia are bright red prior to spore formation but this fades with age and mature annuli are quite normal in colour.

5. **Christella** Léveillé

Smith (1971*b*) published an account of the 17 neotropical species belonging to *Thelypteris* section *Cyclosorus*, following Morton's (1963) concept of the group and three of these taxa have been examined in this survey from Trinidad. The three species are all members of *Christella*. In 1974 Holttum distinguished two sections in the genus, namely *Christella* and *Pelazoneuron*, and later published a monograph of the former (Holttum, 1976). A number of taxa in this section have been investigated cytotaxonomically in some detail by Panigrahi & Manton (1958) and by Ghatak, Manton & Holttum (1971), and these findings are relevant to two of the species considered here, namely *C. hispidula* and *C. dentata*.

C. hispidula is pantropical in distribution and has so far proved to be diploid (n = 36) where sampled, viz. Sri Lanka (Manton & Sledge, 1954), Nigeria and Ghana (Manton, 1959), Borneo and Ascension Island (Ghatak, Manton & Holttum, 1971), and in Florida and Louisiana (Smith, 1971*b*, under the name *Thelypteris quadrangularis* var. *versicolor* (R. St.John) A. Reid Smith). Hybridization experiments by Ghatak, Manton & Holttum (1971) show that these Old World representatives are members at least of a single biological species, although differing from one another morphologically in characters which have often been used to characterise separate taxa, such as presence or absence of anthocyanin in stipe or rachis, presence or absence of a hairy indusium, and the length of hairs. It appears evident that such variation is also found in the New World. The three specimens examined from Trinidad, each from a different locality, however, were similar to one another morphologically and were also diploid with n = 36, 2n = 72.

C. dentata is also very widespread in the tropics and subtropics of the Old World but unlike the preceding species it is naturalized and not native in the Americas. According to Strother & Smith (1970) extensive records indicate that, to all intents and purposes, it appeared in 1930 in Florida and soon after in many islands of the West Indies. Similar rapid rates of spread have occurred in Central and South America. Its spread over this short time span of about half a century is even more remarkable, not only for the distances involved and the areas covered, but also for the numerical abundance of the plant at the present time. It has proved to be an extremely successful colonizer of disturbed habitats and its weedy tendency is amply attested to in cultivation, where its sporelings are liable to invade pots of other species and displace the original occupants unless strictly controlled.

Although Ghatak (1961) and Mitui (1968) reported diploid plants from India and Taiwan respectively, *C. dentata* has proved to be predominantly tetraploid with n = 72 over most of its range, this being the case in Madeira (Manton & Sledge, 1954), Ghana (Manton, 1959), Singapore (Manton in Holttum, 1954), India (Verma & Loyal, 1960; Loyal, 1961; Ghatak, 1962, 1963), Papua New Guinea (Holttum & Roy, 1965) Taiwan (Tsai, 1972), Florida (Smith, 1971*a*), the Dominican Republic (Smith, 1971*b*), and Jamaica (Walker, 1966*a*). Hybridization experiments by Ghatak, Manton & Holttum (1971) indicated that *C. dentata* was conspecific with *Cyclosorus subpubescens* sensu Holttum and that there is a possibility of autoploidy being involved in the origin of this species although the evidence is not decisive.

The third member of this group to be cytologically examined from Trinidad, namely *C. patens*, is the type species of section *Pelazoneuron* which contrasts with section *Christella* in having veins all free and for the most part in lacking elongate glandular hairs on the sporangial stalk. Smith (1971*b*) recognised three varieties of *C. patens* and all the specimens counted from two localities in Trinidad belong to the distinctive var. *patens*. All were sexual diploids with n = 36, 2n = 72. This is the same as had been reported by Smith & Mickel (1977) for Mexican material but differing from Costa Rican plants which were tetraploid (Smith, 1971*b*). Thus, two cytotypes are present in the one morphological variety. Previously tetraploid counts had been recorded for Jamaican plants (Walker, 1966*a*) under the name *Thelypteris patens* (Swartz) Small without varietal distinction. These plants have now been determined as *C. scabriuscula* (C. Presl) A. Reid Smith.

6. Amphineuron Holttum

A. opulentum is a widespread species with a natural distribution ranging from East Africa to Tahiti (Holttum, 1977). It has become established in Central America and especially in the Caribbean islands in recent years, and Kramer (1978) remarks that it provides a rare example of an alien occurring in quite natural vegetation. Specimens from Trinidad agree with plants from Malesia and S.E. Asia as determined and described by Holttum (1977) in having conspicuously yellow glands in abundance along all the veins and which show no difference in size between those on the proximal veins as opposed to those on the distal. The glands may be easily seen with the naked eye if the frond is held obliquely to the light.

These naturalized plants are tetraploid (based on $x = 36$) with $n = 72$ as was also a specimen from Singapore (Manton in Holttum, 1954). The only other species of this genus whose cytology is known is *A. terminans* (Hook.) Holttum, for which a tetraploid form has been recorded from Sri Lanka (Manton, 1953), whilst both diploid and tetraploid forms were recorded in southern India (Bhavanandan, 1968).

XI. ASPLENIACEAE

1. Asplenium L.

Asplenium is well represented in Trinidad where it contains a large range of morphological and habitat types. Of the nine species examined only one proved to be diploid, all the others being at the tetraploid or higher levels. The diploid plant has been identified by C. D. Adams as *A. abcissum* Willd., a member of the complex centred on *A. salicifolium,* which is considered in more detail later. It is close to *A. auriculatum* Swartz ex Hook., Mexican material of which was reported by Mickel, Wagner & Chen (1966) to be tetraploid with $n = 72$.

The very beautiful, highly dissected *A. cristatum* grows in damp situations in dense forest in Trinidad where it takes on an almost filmy habit. Root tips cells showed $2n = c.\ 144$ i.e. at the tetraploid level, a result which is in agreement with that found for Galapagos material by Jarrett, Manton & Roy (1968). Diploid cytotypes have been reported from Florida by Wagner (1963) and Morzenti (1967).

A. serratum superficially resembles the bird's-nest ferns of the Palaeotropics, *Asplenium nidus* agg., although not attaining the dimensions of some of the Asiatic species where the fronds of some Papua New Guinea plants may reach 3 m in length. Numerous simple fronds are produced, forming a basket which is ultimately more or less symmetrical in shape. Field observations made by the author are at variance with the impressions given from descriptions of this species, where it is implied or even stated that the rhizomes are erect (e.g. Proctor, 1977; Posthumus, 1928; Stolze, 1981) and the fronds arranged regularly. My field notes state 'T6164 *Asplenium serratum* (bird's nest habit). On felled tree, many fronds per rootstock. Masses of roots formed, with humus. Rhizome horizontal, turning upwards. T6165 ditto – pickled. T6166 ditto, *c.* 26 fronds.' Examination of the pickled material confirms that growth is asymmetrical, with more fronds being produced to one side of the rhizome than to the other, and later giving a regular basket structure by subsequent adjustment in the manner in which they are held. A sporeling sent to Newcastle by A. C. Jermy in 1974 showed similar features, but unfortunately died before maturation. These features contrast strongly with those of *A. nidus* and its allies where, as Holttum (1974*a*) has shown, the rhizomes are erect and produce the fronds in a very close regular spiral. Wagner (1963) recorded $n = 72$ for a plant of *A. serratum* from Florida, i.e. a tetraploid, which contrasts with the octoploid level reached by the Trinidadian specimen in which crozier material gave $2n = c.\ 288$.

Jarrett, Manton & Roy (1968) reported Galapagos material of *A. serra* to be tetraploid with $n = 72$, and commented that this species is very variable and likely to prove to be a species complex. This view is substantiated by the finding of an octoploid cytotype in Trinidad in which *c.* 288 mitotic chromosomes were counted on a plant growing epiphytically on a trunk of a palm (*Geonoma* sp.).

The highly variable *A. auritum* exists in at least two cytologically and reproductively distinct forms. Sexual tetraploids have been reported from Jamaica (Walker, 1966*a*) and the Galapagos Islands (Jarrett, Manton & Roy, 1968). In addition, an octoploid agamosporous form was also found in Jamaica and quoted under the name *A. auritum* var. *macilentum* (Kunze ex Klotsch) T. Moore, a synonym of *A. auritum* var. *obtusum* Kunze ex Mett. This form also occurs in Trinidad and agrees in all particulars morphologically and cytologically with Jamaican material. Here also 288 univalents are formed at meiosis and perfectly viable spores are produced as a result of the operation of the Braithwaite scheme of sporangial development first described in the *Asplenium aethiopicum* (Burman f.) Becherer complex (Braithwaite, 1964). Some further details of prothallial features may usefully be added here. As appears to be typical of the few agamosporous members which are known to follow the Braithwaite scheme, the prothalli fail to produce antheridia (in sharp contrast to the situation in agamosporous members following the Döpp-Manton scheme). As so often happens in agamosporous ferns in general, large, well-developed scales are formed very soon after initiation of the sporophyte. Indeed, at an early stage of development the scales are much larger than the sporophyte itself. Proctor (1977) has drawn attention to the characteristic rigid nature of the fronds, a character which has been maintained in cultivation at Newcastle over many years in both Jamaican and Trinidadian material. The fronds tend to be almost succulent in texture in contrast to the sexual Jamaican cytotype. In view of the very distinctive morphological and cytological features of this agamosporous plant there would seem to be a valid case for recognising it as a distinct species to which the name *A. macilentum* Kunze ex Klotsch would apply. In cultivation the plant pots are rapidly filled as a result of division by root buds. Silhouettes of the octoploid agamosporous *A. macilentum* from Trinidad and of the sexual tetraploid form of *A. auritum* from Jamaica are shown in Fig. 35A & B together with their cytology (Fig. 35C–E). Some idea of the complexity of the situation may be gained from the remark by Stolze (1981) that in his opinion *A. auritum* s.l. is perhaps one of the most variable species in the genus *Asplenium* and the one most in need of careful monographic study.

A. salicifolium and *A. integerrimum* are two species which are very closely allied but, as Maxon (1908) has shown, are primarily distinguished by the pinnae being auricled and having subcrenate margins in the former case, and by being non-auricled and entire in the latter. It may be noted also that the rhizome scales differ in my specimens in being 25–30 cells broad and fringed with long hairs in *A. salicifolium* and in being much narrower (only 6–8 cells wide) and entire in *A. integerrimum*. Both are cytologically similar in being octoploid with n = 144 in Trinidad although Sorsa (1970) records n = 72 for *A. salicifolium* from Puerto Rico. A third species, *A. subhastatum*, also has the same chromosome number. However, here the fronds are simple and entire, being almost identical in shape and texture to a single pinna of *A. integerrimum*. The spores of these two species are very similar when viewed under the SEM. The question arises as to whether or not *A. subhastatum* is a good species or whether it might only represent a precociously fertile stage in the development of *A. integerrimum*. There is, however, some suggestive evidence on this point. Specimens in C. Christensen's herbarium (BM) collected in Cuba by Frère Clement, no. 1392, are a mixture of *A. integerrimum* and *A. subhastatum*. One plant bears a simple frond, whilst the other two fronds each have an additional small lateral pinna. Another sheet in herb. BM bears a photograph of item 1045 from the Trinidad Botanic Gardens Herbarium, showing fronds ranging from typical forms of one species to the other. In one of the specimens the simple frond bears at the base two lateral protuberances or auricles suggestive of the beginnings of pinnae. Whether these specimens represent a series in the stages of development of *A. integerrimum* which approaches closely the normal form of *A. subhastatum* in morphology, or whether the latter species is really only a particularly precociously fertile stage in the normal development of *A. integerrimum*, can only be determined by growing the two species in cultivation to see if *A. subhastatum* maintains its identity, and by sowing spores of *A. integerrimum* and noting the morphological sequence of the fronds ultimately produced and at which stage of development these fronds become fertile. Until this is done *A. subhastatum* is maintained here as a separate entity, albeit with reservations.

A. hostmannii tends to be a gregarious plant in Trinidad and builds up small populations of

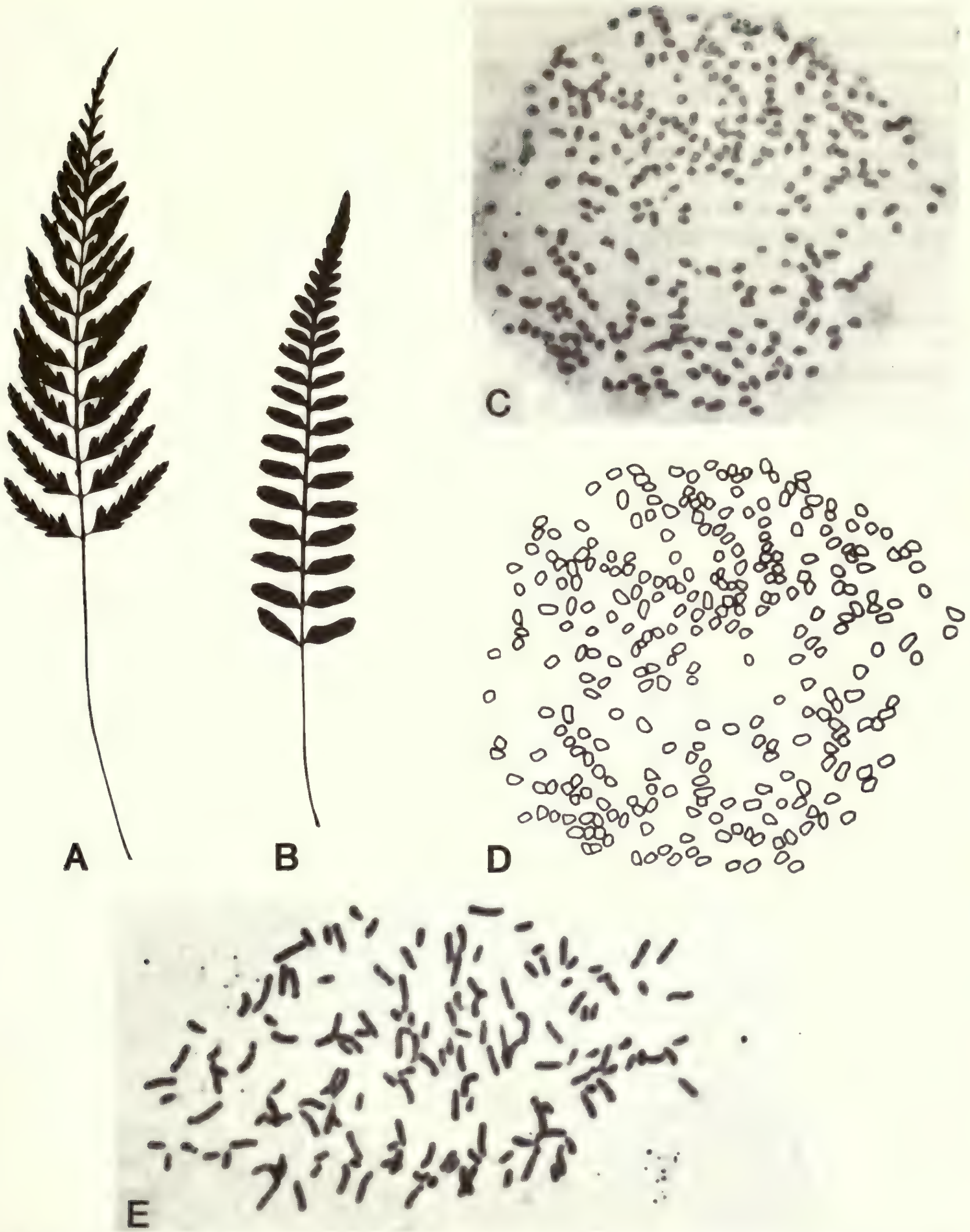

Fig. 35 *Asplenium*. **A**, *A. auritum*, T2502 (Jamaica; 4x sexual) silhouette, × 1/2. **B**, *A. macilentum*, T6834 (Trinidad; 8x agamosporous), silhouette, × 1/2. **C**, *A. macilentum*, T6833, meiosis, 'n' = 288, × 1000. **D**, explanatory diagram of C, 288 univalents, × 1000. **E**, *A. auritum*, T2502, mitosis, 2n = 144, × 1000.

plants by means of root-budding, as has been recorded for *A. plenum* E.St.John ex Small and by Walker (1973*b*) for *A. dentatum* L. *A. hostmannii* is a sexual tetraploid with n = 72, 2n = *c.* 144. Two different hybrids have been found, the other parents being unknown – the search for possible contenders made difficult because of the dominant characters of *A. hostmannii*. The first of the hybrids is a tetraploid with *c.* 144 chromosomes showing irregular pairing at meiosis. The associations were in the form of univalents and bivalents, although the preparations were not good enough on which to base a confident analysis. This tetraploid hybrid is characterized by pronounced hybrid vigour, the fronds at *c.* 40 cm long being twice as long as those of the species. The other hybrid came from Tobago and was triploid with 2n = *c.* 108, again with an irregular meiosis but the chromosomes forming 36 bivalents plus 36 univalents.

In summary, *Asplenium* is represented in Trinidad by a series of high polyploids, no less than six out of the nine species examined being at the octoploid level, whilst by contrast only one is diploid. As in all cases throughout the world where *Asplenium* has been cytologically investigated in some detail there is evidence of hybridization involving several species, and past experience indicates that this is likely to be at a very much higher level than the two hybrid combinations so far found in Trinidad suggest. The overwhelming impression is that the natural variability inherent in several of the groups of closely allied species is further enhanced by gene flow as a result of hybridization, and this has greatly complicated the taxonomic situation.

2. **Diplazium** Swartz

Six species of *Diplazium* have been cytologically examined from Trinidad. Only one, namely *D. caracasanum* was found to be diploid, the remainder being either tetraploids or octoploids. *D. cristatum* and *D. centripetale* both agreed with Jamaican material (Walker, 1966*a*) in being tetraploid, although in the case of *D. centripetale* specimens from the two islands differed slightly in morphology in that Trinidadian specimens lacked the abundant scales which are such conspicuous features on the stipes of Jamaican plants. Similarly, both Jamaican and Trinidadian material of *D. grandifolium* proved to be octoploid, the same applying to *D. striatum* with additional confirmation from Mexico (Smith & Mickel, 1977).

A population of plants from Brickfields proved to be very puzzling. A preliminary examination of meiosis showed that only univalents were present and this could have indicated an agamosporous type of reproduction of the Braithwaite scheme. However, examination of the spores showed them to be crumpled and misshapen, effectively discounting this suggestion and implying the presence of a hybrid population. The univalents are of very different size classes, the long chromosomes being two to three times the length of the short ones (Fig. 36A & B) suggesting the chromosomal constitution of these plants involve very different parental genomes. The overall appearance of the plants was asplenioid, and this appeared to be reinforced by several other features such as the presence of narrow clathrate scales and an X-shaped vascular strand in the upper part of the stipe. Accordingly the name *Asplenium* × *papyraceum* was tentatively assigned to this hybrid, drawing attention to the papery character of the dried fronds. However, detailed cytological analysis showed that instead of the 108 chromosomes which might have been expected of a triploid *Asplenium* hybrid there were, in fact, 123. This number immediately implied a triploid based on x = 41 and hence that instead of it being asplenioid in nature it may well be diplazioid. A careful search was made of the fertile

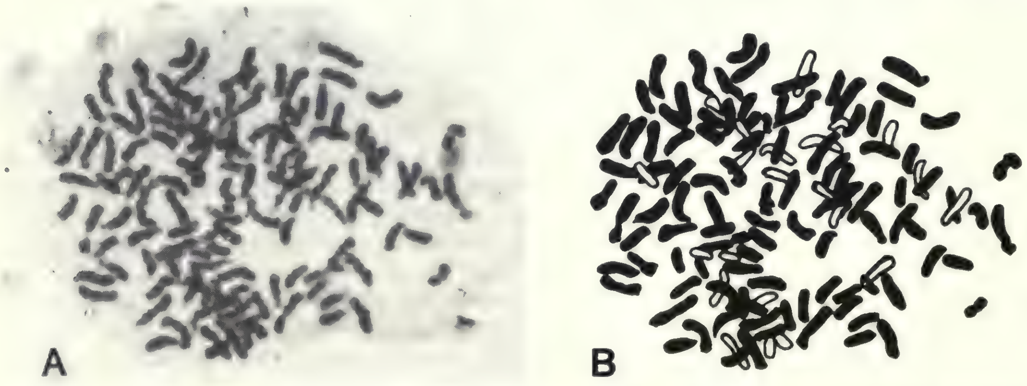

Fig. 36 *Diplazium* ×*papyraceum* (3x). **A**, T6179, meiosis, × 1000. **B**, explanatory diagram, 123 univalents, × 1000.

fronds and several of them showed only the typical asplenioid arrangement of the sori i.e. having a single sorus per vein. However, other fronds did show the double sori characteristic of *Diplazium*. These were very infrequent and could easily be overlooked, especially as there was a tendency for the backwardly-directed member of a pair to be much shorter and hence less conspicuous than the forwardly-directed 'asplenioid' partner. A thorough study was made by A. C. Jermy comparing material of both genera at the BM. Further evidence of the diplazioid nature came in the open grooves of the pinnae connecting with that of the rachis. This hybrid has therefore been named *Diplazium* × *papyraceum* and is morphologically of the *D. caracasanum–D. cristatum* affinity. It has provided a classic example of how cytological information may uncover taxonomic anomalies.

On a world-wide basis there are records for about 70 different taxa of *Diplazium* of which approximately 40% are diploid, the remainder ranging up to the octoploid level of polyploidy. Of the 13 species (excluding hybrids) which are cytologically known from Jamaica (Walker, 1966*a* & 1973*b*) and Trinidad only one (*c.* 8%) is diploid, from which it is evident that polyploidy has played a very significant part in the evolution of the genus in the Caribbean. Cytological information in one species of *Diplazium* is presented in Fig. 37A–C as a basis for comparison with the following genus, *Hemidictyum*.

3. **Hemidictyum** C. Presl

This monotypic genus is represented by *H. marginatum*, which is widely distributed in the American tropics, preferring damp, forested gullies. It is a very large handsome plant with fronds up to 4 m or so in length, the broad simple pinnae being up to 11 or 12 cm wide and clasping the rachis. The pinnae are of an unusual light green colour with a thin lamina which on drying has a fragile membranous nature. The elongate asplenioid sori are located along the straight veins which end in several series of areoles near the margin. The erect, very bulky, rhizome produces numerous thick black fleshy roots. On occasions a large plant may be found occupying a central position amongst several smaller individuals and if the soil is carefully scraped away from these small plants, it is found that many of them originate from the roots of the large parental plant, starting life as root buds in a similar way to those seen, for example, in *Asplenium dentatum* L. and *Ophioglossum* spp.

The cytology is very distinctive indeed, the sporangial cells showing 31 bivalents at meiosis as was first reported for Trinidadian plants (Walker 1973*a* and see Fig. 38) and later confirmed on Costa Rican specimens (F. Wagner, 1980). Further plants from Trinidad clearly show $2n = 62$ in root tip cells, the species thus being a sexual diploid (Fig. 38A–C). The base number of $x = 31$ is a most unusual one, being found neither in *Diplazium* ($x = 41$) nor in *Asplenium* ($x = 36$), two genera to which this species has been ascribed in the past, nor in any of their immediate allies.

The systematic position of *Hemidictyum* has given rise to much discussion, the genus having in the past been included in *Asplenium* by virtue of its soral features and in *Diplazium* to which it shows many resemblances. Lovis (1977) initially placed it in Thelypteridaceae where its chromosome number of 31 would not be out of place in a family which not only has a wide range of morphology but also an aneuploid series of base numbers ranging from $x = 27$ to 36. However, in a note added in proof he defers to Holttum's opinion, given in a personal communication, that *Hemidictyum* is not a thelypteroid fern but comes closest to *Diplazium*, although certainly ranking as a distinct genus. Nevertheless as the matter has been raised the original conflict of opinion is worthy of further consideration and an examination of the various lines of evidence.

One of the most distinctive features of Thelypteridaceae is the invariable presence of acicular unicellular hairs on the upper surface of the rachis and costa (Holttum, 1971: 21). This contrasts strikingly with *Hemidictyum*, in which pubescence of any sort is totally absent.

Pubescence in Thelypteridaceae also extends to the prothalli where, without exception, all cases in the literature report hairs as being present. These commonly are short and papillate, often capped by a yellowish wax, although branched trichomes may occasionally be found. Reports for Old World representatives include those for *Ampelopteris* (Momose, 1941*d*;

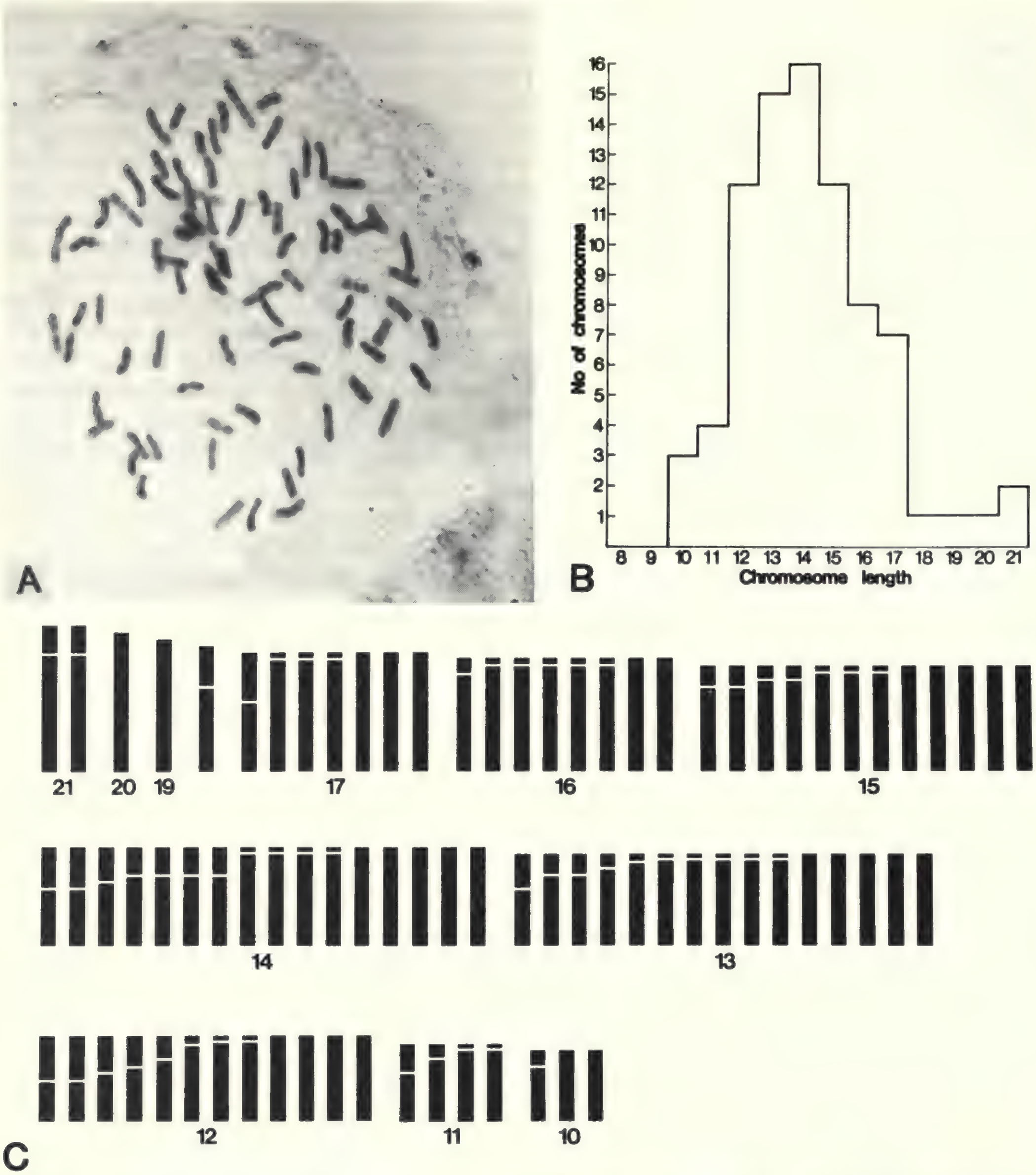

Fig. 37 *Diplazium caracasanum*, J11198 (2x). **A**, mitosis, 2n = 82, × 1000. **B**, histogram of chromosome lengths. **C**, karyogram. Each unit of length = 0·33 μm.

Holttum, Sen & Mittra, 1970), *Amphineuron* (Atkinson, 1975*a*), *Christella* (Momose, 1938), *Coryphopteris* (Atkinson, 1975*a*), *Cyclosorus* (Holttum, Sen & Mittra, 1970), *Macrothelypteris* (Atkinson & Stokey, 1973 – introduced species), *Metathelypteris* (Momose, 1941*b*; Atkinson, 1975*a*), *Phegopteris* (Momose, 1941*b*), *Pseudophegopteris* (Momose, 1941*b*), and *Thelypteris* (Momose, 1941*a*). The wholly or predominantly New World representatives of this family also agree in having hairy prothalli e.g. *Amauropelta* (reported as *Thelypteris*), *Glaphyropteris, Goniopteris,* and *Meniscium* (Atkinson & Stokey, 1973).

Pubescence is not of such universal occurrence in *Diplazium*, being present on the sporophyte of some species and absent from others. Similarly, the prothalli of some species, e.g. *D.*

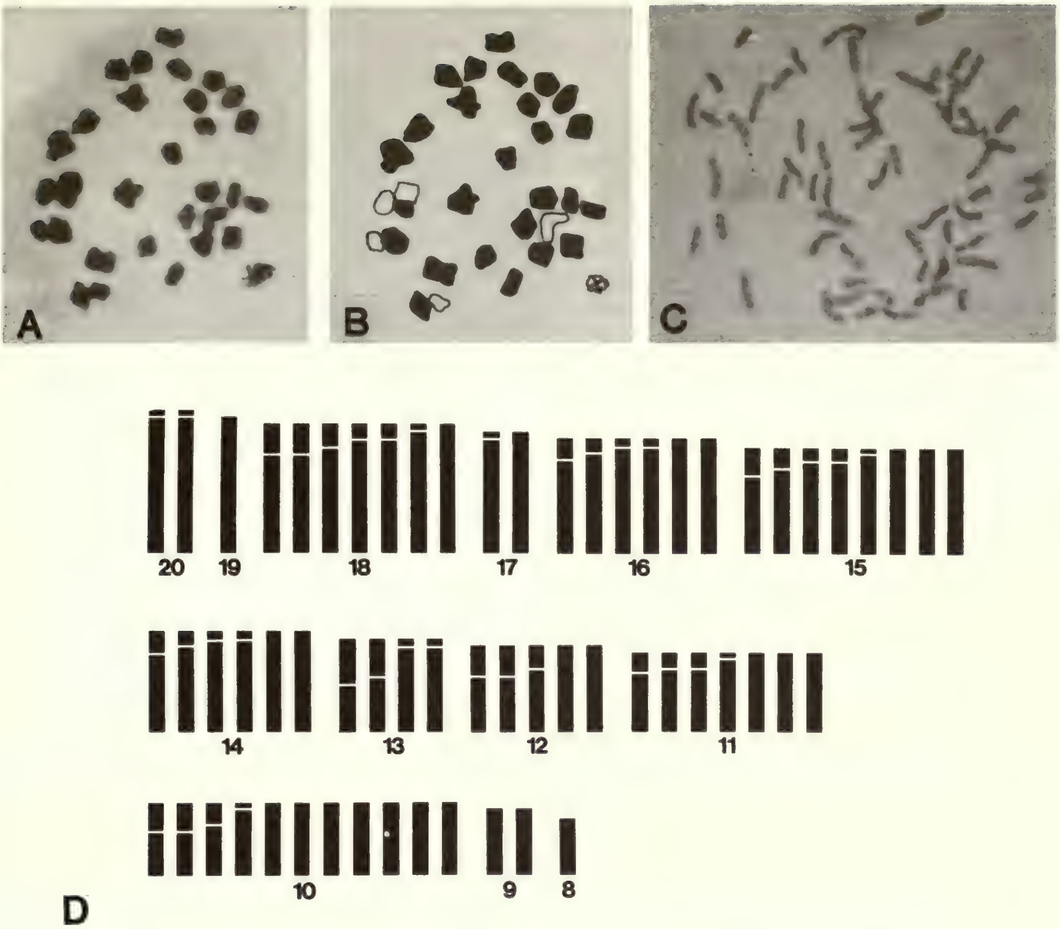

Fig. 38 *Hemidictyum marginatum*. **A**, T10792, meiosis, n = 31, × 1000. **B**, explanatory diagram, 31 bivalents, × 1000. **C**, J11191, mitosis, 2n = 62, × 1000. **D**, karyogram. Each unit of length = 0·33 μm.

stellatopilosum (Brause) Holttum, are hairy (Atkinson, 1967) whilst others, e.g. *D. simplicivenium* (Holttum) Holttum, are naked (Atkinson, 1967; Nayar & Kaur, 1971). Personal observations on a number of Caribbean species of *Diplazium*, e.g. *D. caracasanum, D. centripetale,* and *D. cristatum*, suggest that the naked state is commonplace in the genus.

Stokey & Atkinson (1954), when describing the gametophyte of *Didymochlaena*, mentioned in passing that the prothalli of *Hemidictyum* were naked. Cultures raised at Newcastle confirm this and a few additional facts may be appropriately added. The mature prothalli are symmetrical and cordate with a central apical notch behind which the numerous archegonia are situated. The archegonial necks are erect, and not, as in so many ferns, inclined forwards or backwards. Functional antheridia more or less completely surround the archegonia, except at the very base of the apical notch. When immersed in water the antheridia were seen to discharge spermatozoids, which swam vigorously and appeared to be normal in all respects.

The spores of *Hemidictyum* have a well-marked perispore wing and the surface is furnished with very prominent undulating ridges (Fig. 39B), features which are characteristic of many species of *Diplazium* (e.g. Fig. 39C). Likewise the stipe anatomy is very similar to that found in *Diplazium* species, e.g. *D. esculentum* (Retz.) Swartz, consisting of two more or less parallel and well-separated traces and quite unlike that of *Asplenium*.

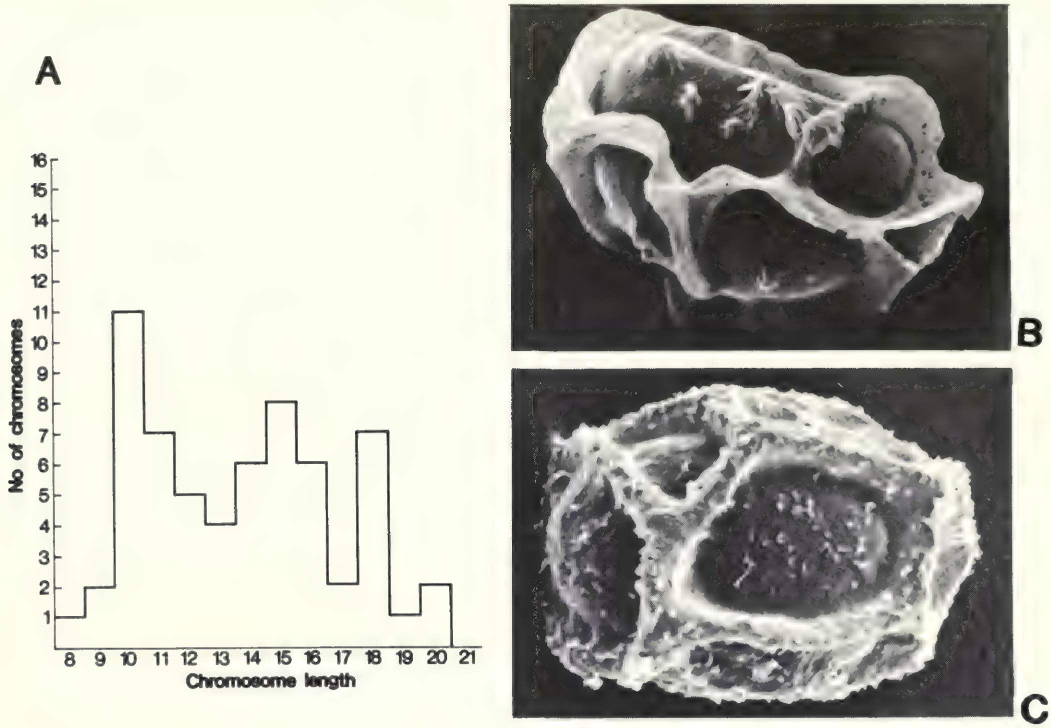

Fig. 39 **A**, *Hemidictyum marginatum*, J11161, histogram of chromosome lengths. **B**, *H. marginatum*, T6410, spore, × 1500. **C**, *Diplazium cristatum*, spore, × 1500.

In his survey of the stomata of ferns van Cotthem (1970) examined those of several species of *Diplazium* and found they were all polocytic, but he did not report on *Hemidictyum*. Here the stomata are also mainly polocytic, although occasional individual stomata may be encountered which are diacytic.

Whilst the chromosome number ($n = 31$) of *Hemidictyum* lies well within the range shown by Thelyteridaceae ($x = 27$ to 36), the simple entire pinnae found in *Hemidictyum* are only to be found in the thelypteroids in those genera which are based on $x = 36$. Holttum (pers. comm.) has pointed out the uniqueness of the venation in the thelypteroids and that anastomosis in this group always relates to the sinus-membrane. He further points out that the scales are very different from those of *Asplenium*, and nearer the ones found in *Diplazium* as regards the marginal cells.

Proctor (1966) reduced *H. marginatum* to a species of *Diplazium*, namely *D. limbatum* (Willd.) Proctor, stating that there were no distinctive characters by which *Hemidictyum* could be maintained as distinct from *Diplazium,* and he continued this practice in his account of the ferns of the Lesser Antilles (1977). Latterly (1980) he has had a change of opinion and recognises *Hemidictyum* as a genus in its own right.

However, whilst there is general agreement that *Hemidictyum* is more closely related to *Diplazium* than to other genera most recent authors, e.g. Copeland (1947), Crabbe, Jermy & Mickel (1975), Pichi Sermolli (1977), Lovis (1977) and Kramer (1978), have maintained it as a distinct genus, the last three authors specifically mentioning the anomalous chromosome number as an important character. Such a large difference in chromosome number ($x = 31$ versus $x = 41$) must inevitably isolate the two genera from one another, effectively preventing any genetic interchange.

The balance of evidence therefore strongly suggests that *Hemidictyum* has developed from a diplazioid ancestry and involving a reduction in chromosome number from x = 41 to x = 31. This exactly parallels the numerical situation reported by Roy & Manton (1966) in *Lomariopsis*, where there is a reduction from 2n = 82 in *L. cochinchinensis* Fée to 2n = 62 in *L. rossii* Holttum (plus other numbers; see under *Lomariopsis*).

An examination of the centromere positions of *Hemidictyum* (Table 16) shows relatively little significant differences between these and those found in a species of *Diplazium* (*D. caracasanum*). However, an inspection of the karyogram (Fig. 38D) of *Hemidictyum* shows a very different situation when compared with that of *D. caracasanum* (Fig. 37C), especially if attention is focused on chromosome length as expressed in the histograms (Figs 37B & 39A). In the case of *Diplazium* the distribution of chromosome lengths is normal, showing a single well-marked peak. This contrasts strikingly with the situation in *Hemidictyum* in which there are at least three well-defined peaks. As we are dealing here with a diploid plant (and not an allopolyploid with parents having three different chromosome size ranges) it is evident that there has been a considerable redistribution of the chromosomal material in the form of translocations. Other evidence (Walker, unpub.) suggests that distortion of the normal monomodal distribution is a common characteristic of ferns which have undergone drastic changes in basic chromosome numbers.

Table 16 Number of chromosomes in each centromere position in *Diplazium caracasanum* and *Hemidictyum marginatum*. (For explantation of symbols see p. 152.)

Position	*Diplazium caracasanum*	*Hemidictyum marginatum*
M	2	0
m	4	4
sm	10	7
st	12	12
t	26	14
T	28	25
Totals	82	62

4. **Ctenitis** (C.Chr.) C.Chr. ex Tardieu & C.Chr.

Ctenitis ampla (Humb. & Bonpl. ex Willd.) Copel. is a name which has been commonly applied to two morphologically similar species with partially overlapping ranges which together stretch from Florida to Central and tropical South America, including the Caribbean Islands. Morton (1968) showed that it was to the species called *Dryopteris nemophila* (Kunze) C.Chr. in Christensen's monograph of *Dryopteris* (1920) that the name *C. ampla* should be correctly applied, the other member of the duo being *C. sloanei*, and he drew attention to some of the features distinguishing the two taxa. These contrasting characters were as follows, those of *C. ampla* being placed first: pinnae short-stalked and pinnules nearly sessile versus pinnae long-stalked and pinnules obviously stalked, pinnule apices obtuse versus attenuate, rhizome scales larger and dark brown versus light brown, and the veins underneath usually lacking glands versus bearing minute glandular hairs. A plant from Jamaica was reported, under the name of *C. ampla*, to be diploid with n = 41 (Walker, 1966*a*). This specimen must now be attributed to *C. sloanei*.

In Trinidad a plant from Aripo valley agreed very closely with Morton's diagnosis of *C. sloanei* and with Jamaican specimens of this taxon but proved to be tetraploid with n = 82 in contrast to the diploid state of the Jamaican plants. It is evident that here two different cytotypes exist in *C. sloanei* which are very similar to one another morphologically and that these in turn form part of a complex which also incorporates *C. ampla*. Two other counts are on record for *C. ampla* s.l., both being diploid, one from the U.S.A. (Wagner, 1963) and the other from Galapagos (Jarrett, Manton & Roy, 1968).

C. protensa was originally described from African material and this species is also a common plant in Trinidad and Guyana. Christensen (1920) considered that although the American form cannot be separated from the African one at the specific level there are nevertheless small differences which he states are worthy of varietal recognition. Chief among these differences are soral characters – the sori being small, near the margin and having persistent indusia in the American variety *funesta* as opposed to the larger, more medial sori which have smaller, deciduous indusia in the African var. *protensa*. Cytologically the African and American varieties appear to be similar, a count of n = 82 being reported by Manton in Alston (1959) for a plant from Ghana and the same number is also recorded here for a specimen from the Valencia Forest Reserve in Trinidad. It is interesting to note the very small difference existing between two such widely geographically separated representatives of a species and it may be no accident in this respect that they are found in West Africa on the one hand and the Guyanan region on the other, two areas that were in intimate contact before the drifting apart of the continents.

A plant of *C. aripensis* which came from the type locality (Aripo Heights) was diploid with n = 41. An additional diploid which showed some similarities to *C. aripensis* but differed in a number of important characters was found on the slopes of El Tucuche and has been described as a new species *C. kallooi* (Jermy & Walker, 1985).

A number of taxa originally reported on cytologically under the name *Ctenitis* have been transferred to *Lastreopsis* and these are detailed in Löve, Löve & Pichi Sermolli (1977). Despite these transferences, cytological records of more than 25 taxa of *Ctenitis* s.str. are available from many countries, approximately 80% of them being at the diploid level, the remainder being tetraploid with the exception of a single triploid. All are based on x = 41.

5. **Lastreopsis** Ching

Lastreopsis was split off from *Ctenitis* by Ching, the distinguishing feature being the nature of the ridging on the upper surface of the frond axes – the ridges being continuous in *Lastreopsis* from one order of branching to another, and being either discontinuous or absent in *Ctenitis*.

Tindale (1965) in her monograph of the genus recognises four subspecies of the widely distributed and variable American *L. effusa*. Jamaican material, reported under the name of *Ctenitis effusa* (Walker, 1966*a*, 1973*b*), was shown to be diploid with n = 41. These plants have abundant yellow glandular hairs on the lower surface of the lamina and are referable to subsp. *effusa*. By contrast, Trinidadian specimens are assigned to subsp. *divergens*, having darker green fronds which for the most part lack the glandular hairs of ssp. *effusa*, although this feature is variable. Cytologically they also contrast with Jamaican material in being sexual tetraploids with n = 82, 2n = 164. It would appear at first sight that there is a good case for raising these subspecies to specific levels, but it is a very polymorphic group and much further study is necessary to delimit specific boundaries. A photograph of the habit of subsp. *divergens* collected by Fendler may be seen in Tindale (1965).

Almost half the species in this genus have been cytologically examined from Australia, Africa, and the Caribbean and all are consistent in having a base number of x = 41 with only the diploid and tetraploid levels being known.

6. **Tectaria** Cav.

In terms of number of individual plants the various species of *Tectaria* form a conspicuous part of the fern flora of Trinidad and the range of variation is such that some specimens present problems of identification. The most distinctive and isolated of all the species is the small, simple-fronded *T. plantaginea*, with a relatively thin creeping rhizome, which is diploid, as is also *T. trifoliata*, the latter having also been reported as diploid in Mexico (Wagner, 1963).

It should be pointed out that the taxonomy and nomenclature of this group is far from clear (Jermy, pers. comm.). There appears a complete range from the more simple ternate leaf with an entire margin (*T. trifoliata*) to the pentaphyllous leaf-form in which the basiscopic lobe is well developed, and with often deeply cut lobes (*T. heracleifolia* – more common in the Greater Antilles) and, according to Proctor (1985), often incorrectly named *T. trifoliata*. Pinnate forms with 2–3 pairs of pinnae are found and Jenman (1909: 202) named Trinidad plants *Tectaria purdiei* (Jenman) Maxon (sub *Aspidium*). Whilst Christensen (1934: 183) equates this with *T. trifoliata*, we believe it is distinct and prefer to maintain it as a separate species.

A population found in dense montane forest on limestone on Aripo Heights (*Jermy* 3002, *Walker* T 7088) was distinct in being of plants of a substantial size and with a glaucous cast to the leaves. This was due to the lamina being covered with short light-reflecting hairs. It is reminiscent of *T. heracleifolia* in colour and leaf margin cutting, but has 5–7 pinnae on a broadly lanceolate frond, and has been named *T. ramkissoonii* (Jermy & Walker, 1985) in recognition of the help and friendship of Roodal Ramkissoon, whose field knowledge of the flora of Trinidad was invaluable. It approaches *T. trinitensis* Maxon in its abundant covering of hairs on both surfaces of the frond although not as dissected as the latter. *T. trinitensis* was not collected during this survey and its cytology is unknown, but it is tempting to suggest a genetic connection between the two species. *T. ramkissoonii* has $n = 80$ chromosomes and hence is tetraploid as is the case with *T. heracleifolia* in Trinidad and also in Jamaica (Walker, 1966*a*, 1973*b*). This latter species has also been noted as tetraploid from Florida (Wagner, 1963) but diploid cytotypes have been reported as occurring in Mexico (Mickel, Wagner & Chen, 1966) and Costa Rica (Gomez-Pignataro, 1971).

The most complex group is that centred on *T. incisa*, where there is not only a range of morphological variation which at the extremes approach other species, but where there are also cytological differences. Sorsa (in Fabbri, 1965) recorded *T. incisa* as being diploid in Peru and as tetraploid (under the synonym *T. martinicensis* (Sprengel) Copel.) from Puerto Rico. Both diploid and tetraploid forms occur in typical *T. incisa* from Jamaica (Walker, 1966*a*), but in Trinidad all the specimens examined were uniformly tetraploid. Smith & Mickel (1977) noted, under the name *T. incisa*, a specimen sent from Trinidad by Dr Fay as being diploid. As no voucher specimen can be found (Mickel, in litt.) the true identity of this record is in doubt. However, here the situation is complicated further by the presence of a morphologically distinctive diploid entity, sometimes known as *T. incisa* var. *vivipara*, which differs from the diploid Jamaican form mentioned above. The former tends to have narrow pinnae (*c.* 2·5 cm wide) and the bulbils produced in the axils of the upper pinnae are a prominent feature of the plant when well-developed, especially when seen growing in wet situations. Even where the bulbils on a particular frond are not well-developed, the position of the young initials may be detected by the presence of small clusters of dark scales.

Trinidadian material of this diploid is further distinct in having on the underside of the leaf numerous, short (2–3-celled) hairs on the costae and larger veins (and occasionally on the lamina itself in the region of the costa). Viviparous forms from Central and South America however lack these hairs, and have also a gross morphology resembling tetraploid *T. incisa*. Tetraploid *T. incisa*, common throughout Trinidad in a typical and easily recognisable form, is rarely pilose beneath and, if so, then only at the very base of the pinna. *T. incisa* var. *vivipara* has been redefined at specific rank under a new type of which the cytology is known (Jermy & Walker, 1985).

T. vivipara has been found in the Brickfield population to hybridize with tetraploid *T. incisa* to give a triploid (*Walker* T6175) which forms up to *c.* 40 bivalents and 40 univalents at meiosis in some cells, others showing virtually all univalents. It has been named *Tectaria* ×*bulbifera* (Jermy & Walker, 1985), is very vigorous and is larger than *T. vivipara*, with broader pinnae and lacking the short hairs on the underside of the costae, more characteristic of *T. incisa*. It inherits the viviparous habit and as a consequence can increase in numbers despite the irregular meiosis leading to inviability of the spores. Silhouettes of the hybrid and two parents are given in Fig. 40A–C.

A fourth entity of the *Tectaria incisa* complex collected near Brasso Secco by A. C. Jermy (J 10941), and grown to maturity at Kew, proved to be a diploid with $2n = c.\ 80$. The lamina of the fronds is as broad as it is long, with usually only two pairs of pinnae, giving an overall orbicular

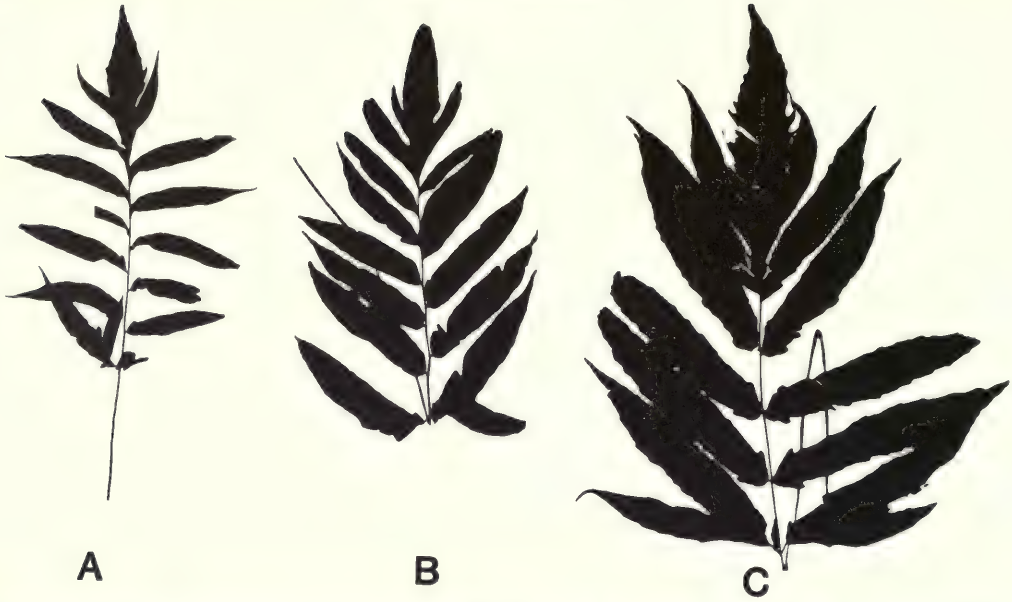

Fig. 40 *Tectaria*. **A**, *T. vivipara*, T6173 (2x), silhouette, × 1/8. **B**, *T.* × *bulbifera*, T6175 (3x) silhouette, × 1/8. **C**, *T. incisa*, T6972 (4x), silhouette, × 1/8.

outline, in contrast to the ovate-laceolate fronds with several pinnae seen in other members of the complex. The taxon has been named *T. orbicularis* (Jermy & Walker, 1985).

7. **Hypoderris** R.Br. ex Hooker

All our specimens of this monotypic genus were gathered in very damp, deeply shaded situations and had a somewhat fleshy texture in all parts, including the creeping rhizome. The simple fronds with sagenoid venation vary from being only slightly lobed at the base to being prominently hastate. In some cases this lobing almost takes the form of a pair of pinnae. The sori are scattered on the under surface of the frond and each is protected in the early stages by a fimbriate indusium which is soon hidden by the developing sporangia and requires careful searching to find in fully mature specimens.

Although *Hypoderris* has been considered as being closely related to *Woodsia* (Bower, 1928) on account of its indusial characters, in nearly all other respects it is tectarioid, and modern opinion is virtually unanimous in placing this genus close to *Tectaria*.

The chromosome numbers of $n = 40$, $2n = 80$ (Walker, 1973*a*) are in complete agreement with a tectarioid origin (Fig. 41A–D). The spores are furnished with prominent toothed spines (Fig. 41E) similar to those found in some species of *Tectaria*.

8. **Cyclopeltis** J. Smith

This genus was typified on Jamaican material collected by Swartz. It has a disjunct distribution throughout the tropics, being absent from Africa and southern India (Holttum, 1954) and is variously treated as being either monotypic or comprising a small number of species. Trinidadian material is morphologically identical with that from Jamaica and also agrees (Walker, 1966*a*) in being diploid with $n = 41$.

9. **Didymochlaena** Desv.

This pantropical genus is usually regarded as monotypic, although Christensen (1934) recog-

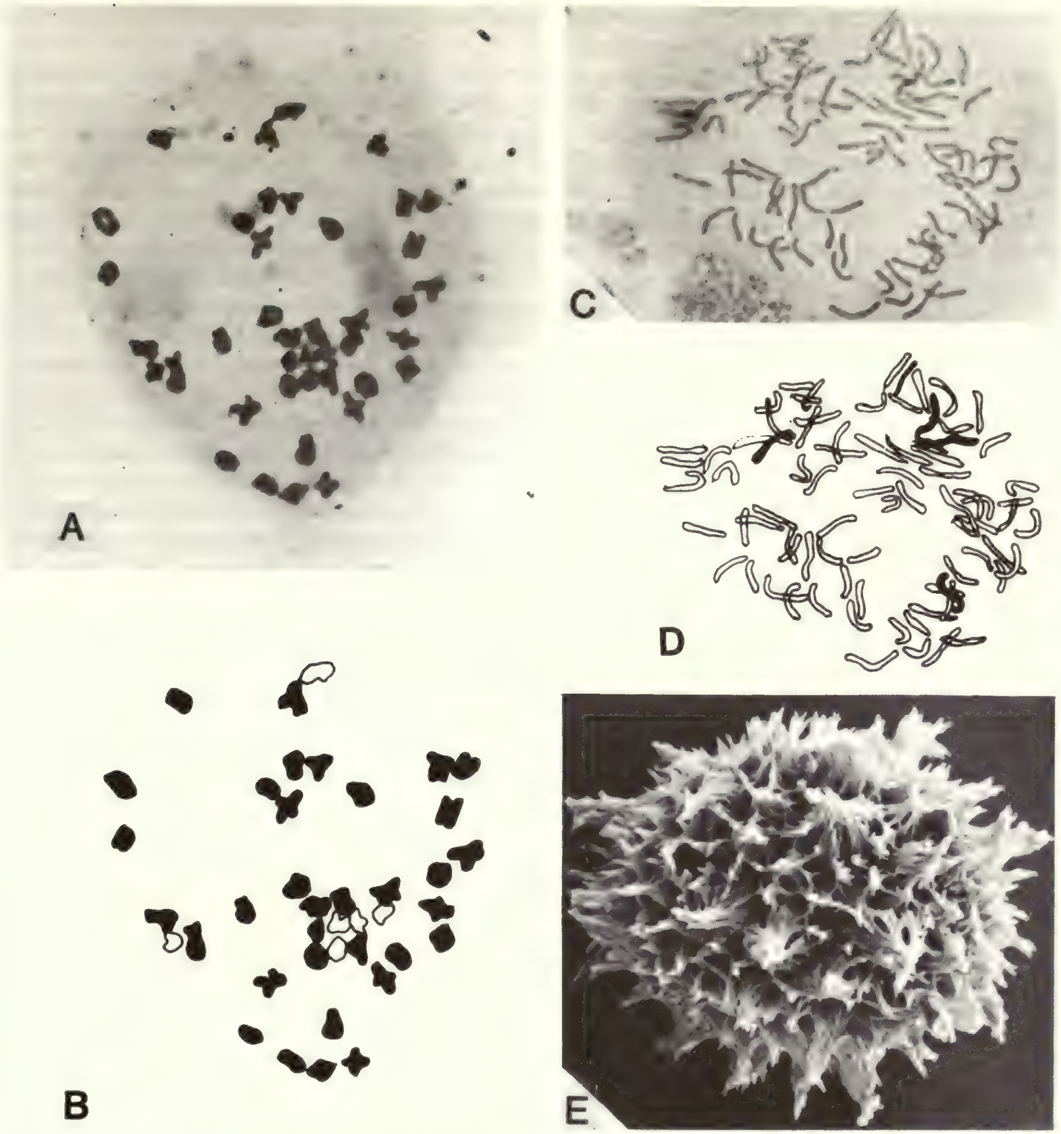

Fig. 41 *Hypoderris brownii.* **A**, T6205, meiosis, × 1000. **B**, explanatory diagram of A, 40 bivalents, × 1000. **C**, T6205, tapetal mitosis, 2n = 80, × 1000. **D**, explanatory diagram of C, × 1000. **E**, spore, × 1500.

nised two species in Madagascar, and Holttum (1954) considers that more local species may be recognised wherever the genus has been more intensively studied.

The basic chromosome number is x = 41 and previous counts have been established on material from Malaysia (Manton in Holttum, 1954), Costa Rica (Gomez-Pignataro, 1971) and Mexico (Smith & Mickel, 1977). All proved to be diploid and the same is true of the Trinidadian material reported here. A further count, extending the geographical range, has proved to be n = 41 (and therefore also diploid) for a plant from Papua New Guinea (Walker, unpublished).

10. **Polybotrya** Humb. & Bonpl. ex Willd.

This tropical American genus comprises some 25 species of which four occur in Trinidad. All are conspicuously dimorphic, the fertile pinnae being almost devoid of lamina and covered, at least on their lower side, by naked sporangia.

Polybotrya cervina is anomalous in a number of features, such as in being completely terrestrial normally with a thick, short, creeping rhizome. The other species pass through an initial terrestrial stage in which the rhizomes are thin (*c.* 8 mm diameter) and the fronds relatively small and sterile. After making contact with a tree trunk the rhizomes thicken considerably (to *c.* 25 mm diameter), become scandent and produce large fronds, some of which may be fertile. A further distinction is that the veins of *P. cervina* are joined by an inframarginal commissure in contrast to the entirely free state found in some of the other species.

Most authors consider these characters to be insufficient to justify generic recognition, but Pichi Sermolli (1977) upholds the separation of this species as the sole member of the genus *Olfersia* of Raddi. It should be noted that the distinction between the typically terrestrial habit of *P. cervina* and the scandent habit of the other members of the genus may occasionally break down. My field notes for a specimen of *P. osmundacea* (T6426) state 'this specimen unusual in that it was fertile whilst still terrestrial in deep leaf mould'. Anatomically, *P. cervina* is similar to *P. osmundacea* (Walker, unpub.); it is very easy to cultivate in pans and readily becomes fertile grown in this manner, unlike the other species which require the stimulus of climbing.

Eight specimens of *P. cervina* have been cytologically examined from several localities in Trinidad and agree with Jamaican representatives in being sexual diploids with $n = 41$, $2n = 82$ (Walker, 1966*a*; fig. 40). Smith & Mickel (1977) also noted an unlocalised specimen from Trinidad as being diploid. Similarly, *P. osmundacea*, also examined from Jamaica (Walker, 1966*a*; fig. 41) was diploid with $n = 41$. In this species there is also a certain amount of instability in the expression of frond dimorphism, in which occasionally fertile parts appear on vegetative-type fronds. In one specimen, of an otherwise typically vegetative frond, the lowest pinna was completely fertile and the basal half of the adjacent pinna was sterile whilst its upper half was fertile. A specimen behaving in a similar way was also collected in Jamaica. The third species examined, *P. caudata*, was also sampled from several localities and likewise proved to be diploid.

Nearly all modern systems agree in placing *Polybotrya* among the dryopteroid ferns next to the monotypic *Maxonia* to which it is morphologically similar in a number of features, including the separate and distinctive terrestrial and scandent phases. They also have the basic chromosome number of $x = 41$ in common. The two genera differ in soral characters, *Polybotrya* having naked acrostichoid sporangia as compared with the discrete sori of *Maxonia* which are protected by reniform or rounded indusia. Glands which are present on the sporangial stalks of *Polybotrya* appear to be absent from *Maxonia*.

Anatomically (Walker, 1972, and unpub.) there are great similarities between the two genera for example in the structure of stipe and lamina. In particular, transverse sections of the rhizome of *Polybotrya cervina* and the scandent form of the rhizome of *Maxonia* are virtually identical, even to the presence of numerous small groups of exceptionally thick-walled cells with conspicuous pitting and which are randomly scattered in the ground tissue. In both genera the spores are very densely and minutely spinulose.

11. **Bolbitis** Schott

Although chromosome counts are available for some 19 species of *Bolbitis* (including some which were formerly ascribed to *Eganolfia*), together with a number of additional cytotypes and interspecific hybrids (see summary in Hennipman, 1977) only two have been recorded from the New World tropics. These are for *B. pergamentacea* and *B. aliena* from Jamaica (Walker, 1966*a*) which proved to be diploid and tetraploid respectively. To this very short list two more species, together with a further cytotype may be added.

Two plants of *B. portoricensis* from the same locality showed $2n = 82$ at mitosis and are therefore diploid. However, *B. hemiotis* collected by both A. C. Jermy and T. G. Walker on different occasions from the same small area in a gully in Aripo Valley showed cytological differences. Two specimens were diploid, whilst the third was tetraploid. In gross morphology this tetraploid differs in no way from the diploid, and even at low magnification the differences between the cytotypes are relatively slight. The rhizome scales are light brown and measure approximately 1·5 mm × 4 mm in the diploid, as compared with the dark brown and rather larger scales (*c.* 1·5 mm × 7 mm) of the tetraploid. In addition small glandular hairs *c.* 3 cells long are very evident on the under surface of the frond of the tetraploid, whilst being much less evident or even lacking in the diploid. However, stomatal lengths are conspicuously different in the two cytotypes, those of the diploid having a mean of 67·5 μm (56·5 to 76·0 μm) compared with a mean of 79·0 μm in the tetraploid (60·0 to 90·0 μm). Measurements of stomatal lengths of four other plants from the same population suggests that the diploid state is the normal and that the tetraploid may be an individual plant, possibly of very recent origin. The almost identical superficial appearance of the two cytotypes suggests that here one may be dealing with an autotetraploid, and this view is strengthened by the lack of any other species in the vicinity which is remotely like *B. hemiotis* with which it may have contributed to an alloploid origin. It is of interest to note that Hennipman (1977: 54) comments that, in the case of the Asiatic triploids, the morphological differences are trifling as compared with the diploids and he considers these to be of an autoploid nature. Some further support for this theory may be seen in some of my preparations of triploid plants of *B. quoyana* from Papua New Guinea, where trivalents are present in addition to the univalents and bivalents, which form the bulk of the chromosome associations. The same is also true of preparations of *B. sinuata* (C. Presl) Hennipman from Sarawak (Walker, unpub.).

The sporangia of the Trinidad tetraploid *B. hemiotis* were fixed in the field and proved to be too young to be undergoing meiosis, and the presence or absence of multivalents which may have provided more direct evidence of the type of polyploidy involved could not therefore be determined. Some of the tapetal or archesporial cells were undergoing mitotic divisions and it is upon these cells that the cytological record is based.

All records to date for *Bolbitis* throughout the world have been at the diploid, triploid, or tetraploid levels and without any evidence of agamospory. The strong tendency for the genus to produce bulbils (three quarters of the species according to Hennipman, 1977) may help to account for the persistence of large numbers of otherwise sterile triploid plants in local populations in different parts of the world, and may be a contributory factor in the maintenance of autopolyploids.

12. **Lomariopsis** Fée

This genus of large scandent ferns is widespread in the tropics including the Pacific, Asia, Africa, and the New World. Copeland (1947) expressed doubts as to whether or not the American group was properly included with the Old World species, but he did not elaborate on this brief comment. The general morphology, habit, and anatomy do not appear to me to indicate any major discontinuity.

Chromosome counts have been recorded for only five species (Manton, 1959; Roy & Manton, 1966), four of which are African in origin and are quite clearly anomalous in showing a reduction series from the base number of x = 41 shown by the Asiatic *L. cochinchinensis*.

Here there is a reduction in chromosome number from 2n = 82 in diploid members of the family via *L. guineensis* (L. Underw.) Alston with 2n = 78, to 2n = 62 in *L. rossii* Holttum and to 2n = 32 in *L. hederacea* Alston. In the case of *Lomariopsis* the two lowest numbered species show striking differences in chromosome size and shape, due, in Lovis' (1977: 295–297) opinion, to translocations leading to a refashioning of the karyotype and a reduction in number. No chromosome counts have previously been available for American material, and the two specimens of *L. marginata* which were examined from widely separated localities in Trinidad proved to be diploid with n = 41. This is in agreement with the Asiatic *L. cochinchinensis* and a cell is illustrated in Fig. 42A & B. The confirmation of x = 41 as the primary base number in *Lomariopsis* helps to underline the affinity of the genus with other members of the subfamily Lomariopsidoideae *sensu* Holttum or with Lomariopsidaceae of other authors.

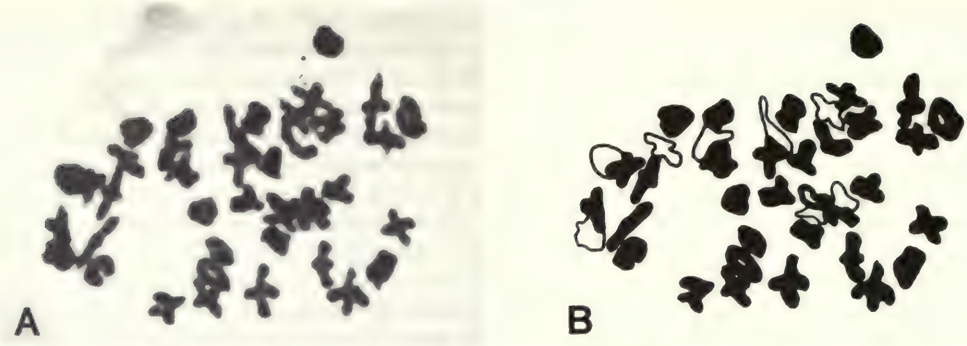

Fig. 42 *Lomariopsis marginata*, T6214. **A**, meiosis, n = 41, × 1000. **B**, explanatory diagram, 41 bivalents, × 1000.

13. **Elaphoglossum** Schott ex J. Smith

The chromosome numbers of the majority of the species of *Elaphoglossum* in Trinidad have been determined and all have proved to be at the diploid level. Six of these are new records and the two that have been counted from elsewhere also agree in being diploid, namely *E. crinitum* from Puerto Rico (Sorsa, 1966) and Jamaica (Walker, 1966*a*, 1973*b*) and *E. rigidum* (under the name *E. flaccidum* (Fée) T. Moore) from Puerto Rico (Sorsa, 1966, 1970). This absence of polyploidy contrasts markedly with the situation in Jamaica where four of the 11 species examined were tetraploid (Walker, 1966*a*, 1973*b*).

The members of this genus, despite a high proportion of them being epiphytes, are very amenable to pot culture provided that adequate drainage is provided. Over the course of many years it has been noted that their behaviour in cultivation closely parallels that seen in the wild. Thus, species which are frequently collected in the fertile state in the wild normally produce fertile fronds freely in cultivation, e.g. *E. rigidum*; conversely *E. herminieri* as a pot plant only becomes fertile at infrequent intervals, sometimes several years elapsing between one crop of fertile fronds and another, a type of behaviour which doubtless accounts for the fact that it is most commonly found in the sterile state in nature. This type of behaviour is common to many species, an appreciable number of which have been described from sterile material. Their amenability to cultivation, coupled with the retention of their wild characteristics, suggests that here is a group which may form admirable material for investigating the factors which affect or induce fertility.

Fée created the genus *Hymenodium*, of which *H. crinitum* (L.) Fée was the sole representative, on the basis of the anastomosing veins present, in contrast to the free ones of *Elaphoglossum*. However, the venation is the only distinguishing feature, and in all other respects such as spore morphology, gametophyte development, cytology, etc., *H. crinitum* is a true *Elaphoglossum* and is considered as such here. One of the most conspicuous features of *E. crinitum* is the presence of conspicuous, shiny, black scales, somewhat like eyelashes, which clothe the stipe and fronds. Two plants growing side by side on El Tucuche behaved rather differently in respect of scales. One was quite typical in having scales present on the frond surfaces in addition to the margins, rachis, and stipe (T10990), whilst the other plant differed only in lacking scales on the frond surfaces (T10989). Both plants were sent alive to Newcastle in 1966 and have retained this habit even since, the striking difference in appearance being due to a simple developmental event. The young fronds produced by both plants are at first identical with abundant scales being present on all parts. However, the scales of T10989 soon drop off the upper and lower surfaces of the lamina, whilst persisting elsewhere, including the margins. This is in contrast to those of T10990 which persist throughout the life of the frond. This suggests that scale distribution may be under relatively simple physiological/genetical control, and it is tempting to speculate whether or not in the evolutionary history of the species of *Elaphoglossum* which characteristically have scales more or less confined to the margins of their fronds, the scales had been present on the frond surfaces and then later were lost except at the margins, rather than having been produced only in this highly specialized marginal position from the very beginning.

Elaphoglossum produces few aberrations in cultivation, a simple forking of the frond being the most common form. In one instance *E. crinitum* produced a frond which was intermediate between a fertile and sterile one, with the sporangia spreading along a broad marginal band for about 2/3 of the way up, leaving a broad, sterile, central and upper area.

14. **Oleandra** Cav.

Oleandra has the bulk of its 40 or so species in the Asiatic and Pacific areas, with only a very few representatives extending to Africa and America. *O. articulata* is the only American species which has been cytologically examined and is diploid with n = 41 in Jamaica (Walker, 1966*a*) and Puerto Rico (Sorsa in Fabbri, 1965; Sorsa, 1970). A specimen which was scandent on a palm trunk at the edge of Aripo Savanna was also diploid. This species lacks the somewhat soft hairy nature and characteristic odour possessed by many other members of the genus.

15. **Nephrolepis** Schott

All 14 species of *Nephrolepis* which have been cytologically examined from various parts of the world have been diploid, although two, namely *N. hirsutula* (G. Forster) C. Presl and *N. pectinata* (Willd.) Schott, also have tetraploid cytotypes as reported by Walker (1966*a*) and Kuriachin (in Fabbri, 1965) respectively.

The Trinidadian specimens of the pantropical *N. biserrata* were also diploid as has been shown to be the case in three continents viz. Asia (Ghatak, 1962, 1963; Abraham, Ninan & Mathew, 1962), Africa (Manton, 1959) and America (Sorsa, in Fabbri, 1965; Sorsa, 1970; Walker, 1966*b*). Similarly, the purely American *N. rivularis* showed n = 41.

XII. BLECHNACEAE

1. **Blechnum** L.

The most numerous members of *Blechnum* in Trinidad in terms of species are those belonging to the *B. occidentale* affinity, all of which have a basic chromosome number of x = 31. This places them cytologically approximately in a mid-position in the genus which shows a series of base numbers from x = 28 to x = 36.

B. occidentale often occurs in large stands which are at least partially a consequence of the stoloniferous habit of the species. All plants examined from a number of different localities in Trinidad and Tobago were sexual tetraploids with n = 62, 2n = 124 (Fig. 44A & G). This is also the case in Jamaica (Walker, 1966*a*, 1973*b*; Smith & Mickel, 1977), Mexico (Smith & Mickel, 1977), Galapagos (Jarrett, Manton & Roy, 1968) and in Texas, U.S.A. (Walker, unpub.). Sorsa's report (1970) shows a slight discrepancy in that he records n = 64 instead of 62 for this species from Puerto Rico; nevertheless, it is clearly still at tetraploid level.

A further member of the complex is *B. fraxineum*, which has two cytotypes in Trinidad, both of which are sexual, one being diploid with n = 31, 2n = 62 (Fig. 44B & H), and the other tetraploid with n = 62, 2n = 124 (Fig. 45A). Comparing the morphology of the limited amount of cytologically investigated material, there seems to be a tendency for the fronds of the tetraploid to be rather narrower and to have somewhat more pinnae (*c.* 3 pairs) than in the diploid with only one or two pairs. A further tendency is for the stipe and rachis of the diploid to be deeper red than in the tetraploid. How far these are reliable features needs further investigation, but silhouettes of living material are shown in Fig. 43A & B. Spore length differences may be a more reliable character, as they gave consistent results in the five samples measured, the spores of the tetraploid being approximately one third as long again as those of the diploid (Table 17). This contrasts with the situation as regards stomatal length which is virtually the same in the two cytotypes, as are also rhizome scale characters.

The very close morphological similarities existing between the diploid and tetraploid forms of *B. fraxineum* immediately raises the suspicion that the tetraploid may be autopolyploid in

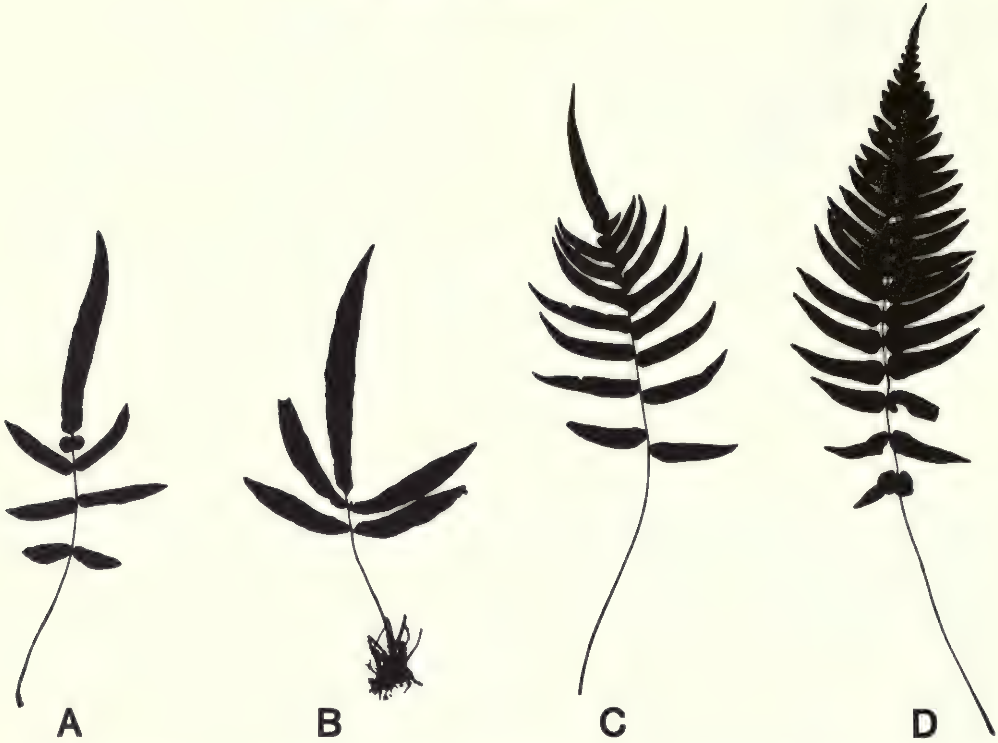

Fig. 43 *Blechnum*, silhouettes of fertile fronds, × 1/4. **A**, *B. fraxineum*, NY6 (4x). **B**, *B. fraxineum*, T6243 (2x). **C**, *B.* × *caudatum*, T7232 (3x). **D**, *B. occidentale*, J11359 (4x).

origin. If this is indeed the case, then its karyotype would be expected to show each type of chromosome found in the diploid to be represented four times. As may be seen from Table 18 the pattern of distribution of centromere positions is quite differerent overall, the corresponding figures for the diploid and tetraploid plants not being in a two:four relationship. A closer inspection of the karyograms (Figs 46B & 47B) reinforces this impression and hence it is highly probable that, in the case of *Blechnum fraxineum*, we are dealing with an allo- rather than an auto-tetraploid. If the assumption is made that the close similarity in morphology between the diploid and tetraploid forms is a consequence of the former being part-parental to the latter, then it should be possible to make some predictions concerning the other, as yet unknown, diploid parent involved in the ancestry of the allotetraploid. Although little can be said about the morphology of the unknown parent because of the dominance of the characters in the diploid, except to suggest that its frond may have more numerous pinnae and be narrower than those of the known diploid, it should possess a characteristic karyotype. A close approximation to what this is may be arrived at by subtracting the figures in each centromere group of the known diploid from the corresponding figures of the tetraploid. When this is done (Table 18) it will be seen that the two diploid karyotypes, the known and the unknown, differ markedly one from another and are quite distinctive. This prediction should also help to provide a test for the validity of the method if and when the second diploid is found.

In some areas of the Maracas river valley *B. occidentale* occurs in quite large patches, with diploid *B. fraxineum* growing in close proximity. Intermingled with *B. occidentale* are plants which at first sight may be taken for this species, but which have many fewer pairs of pinnae and whose fronds abruptly terminate in a large entire pinna (Fig. 43C). These plants have been taxonomically recognised as *B. caudatum* or *B. occidentale* var. *caudatum*. However, all the plants examined cytologically proved to be sterile triploids, with 2n = 93 (Fig. 45B) and with

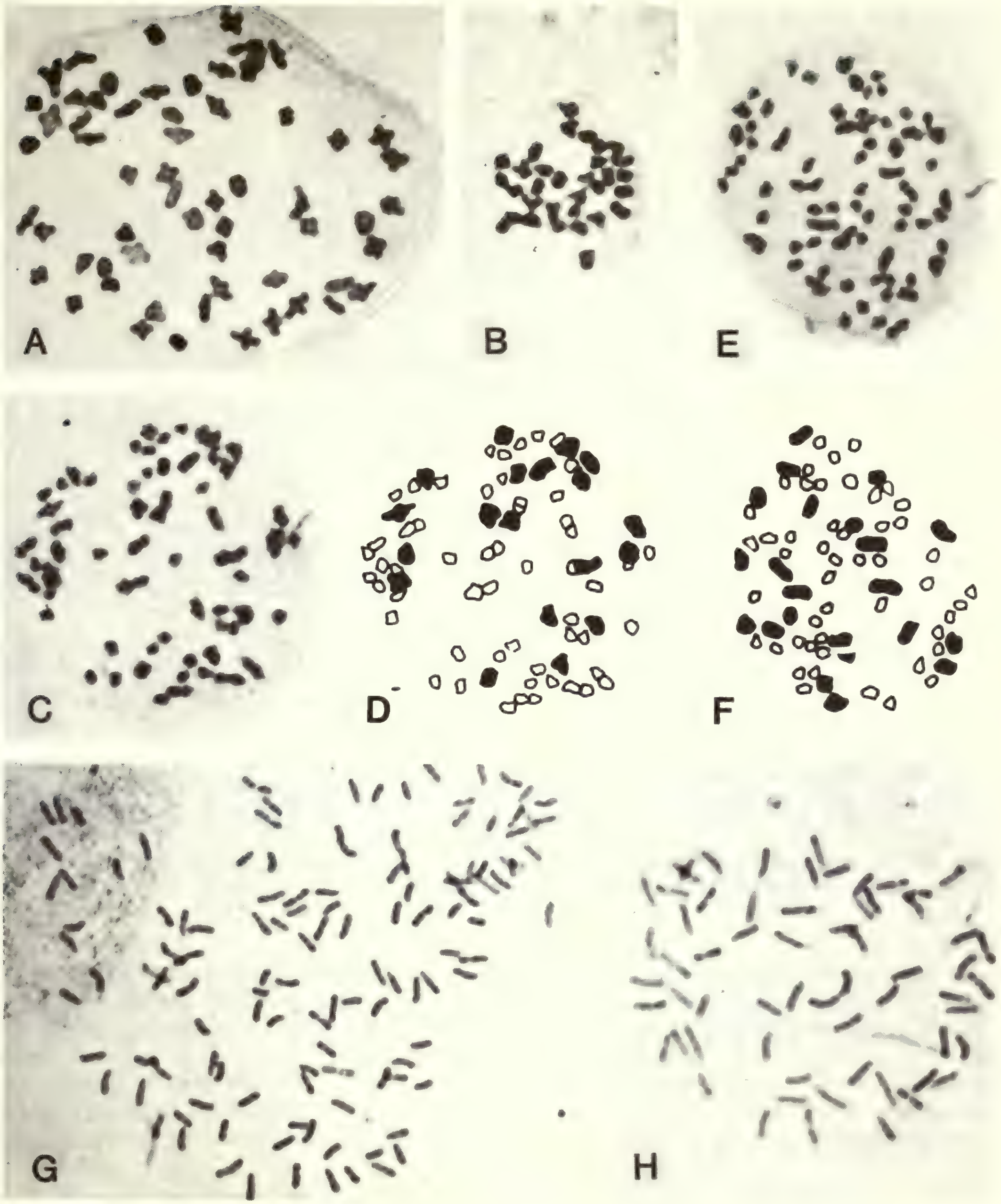

Fig. 44 *Blechnum*. **A**, *B. occidentale*, T6137 (4x), meiosis, n = 62, × 1000. **B**, *B. fraxineum*, T6243 (2x), meiosis, n = 31, × 1000. **C**, *B.* × *caudatum*, T10717 (3x), meiosis irregular, × 1000. **D**, explanatory diagram of C, 19 bivalents (solid) + 55 univalents (outlined), × 1000. **E**, *B.* × *caudatum*, T10717 (3x), meiosis irregular, × 1000. **F**, explanatory diagram of E, 22 bivalents (solid) + 49 univalents (outlined), × 1000. **G**, *B. occidentale*, J11283 (4x), mitosis, 2n = 124, × 1000. **H**, *B. fraxineum*, J10981 (2x), mitosis, 2n = 62, × 1000.

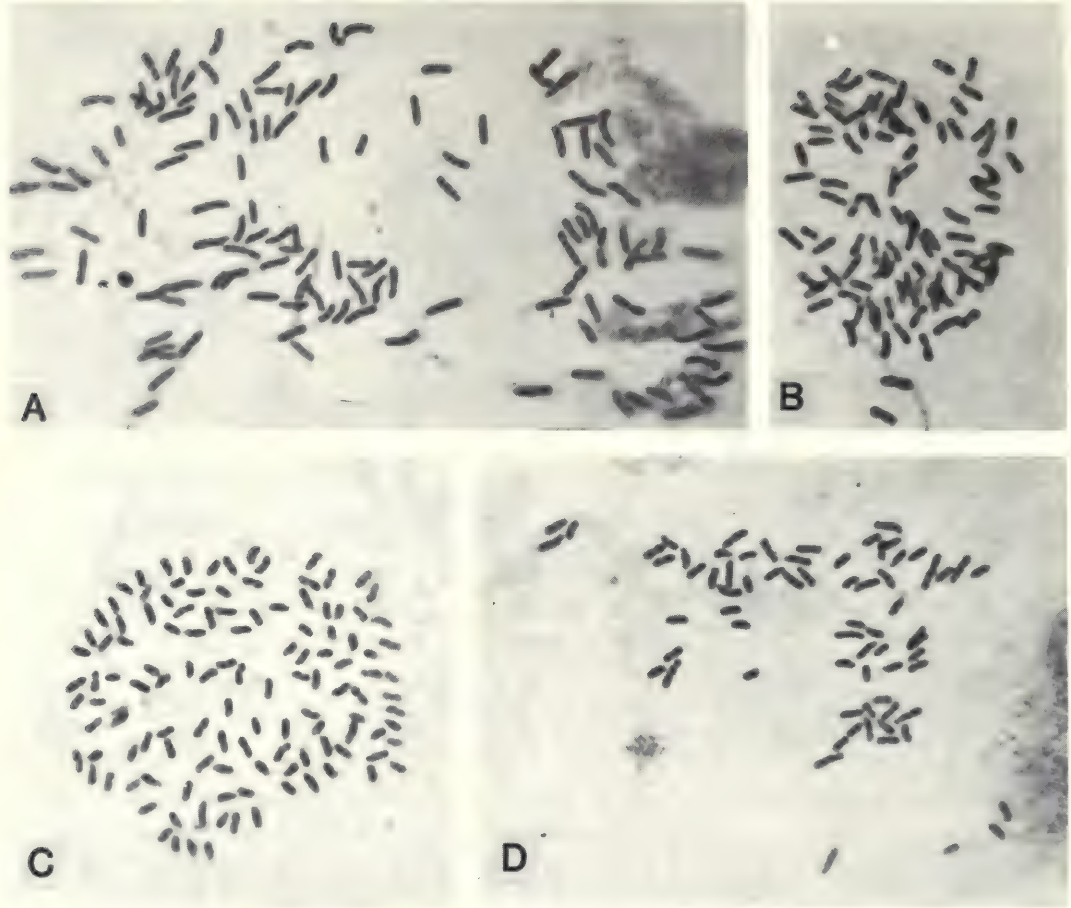

Fig. 45 *Blechnum*. **A**, *B. fraxineum*, NY6 (4x), mitosis, 2n = 124, × 1000. **B**, *B. antillanum* (= × *caudatum*), T4136 (Jamaica; 3x), mitosis, 2n = 93, × 1000. **C**, *B. unilaterale*, T4439 (Jamaica; 4x), mitosis, 2n = 124, × 1000. **D**, *B. serrulatum*, J11215 (2x), mitosis, 2n = 72, × 1000.

irregular meiosis resulting from the formation of a mixture of univalents and bivalents (Fig. 44C–F). As may be seen in Table 19 the number of bivalents ranges widely but nowhere reaches that of a full genome (x = 31). The cytological and gross morphological evidence, together with the fact of association, overwhelmingly indicates that *B. caudatum* is not a species but is a triploid hybrid formed between the tetraploid *B. occidentale* and the diploid cytotype of *B. fraxineum*. The plant is also intermediate in respect of scale characters, those of diploid *B. fraxineum* being narrow and dark brown with thickened cell walls in the centre which become

Table 17 Length of spores in *Blechnum fraxineum* in μm.

Collection no.	Mean	Min.	Max.
4*x* cytotype			
NY6	47·0	41·0	56·0
NY3	49·0	41·0	59·0
2*x* cytotype			
Fay s.n.	36·0	33·0	44·0
T6243	36·0	33·0	44·0
ACJ 10981	37·5	33·0	44·0

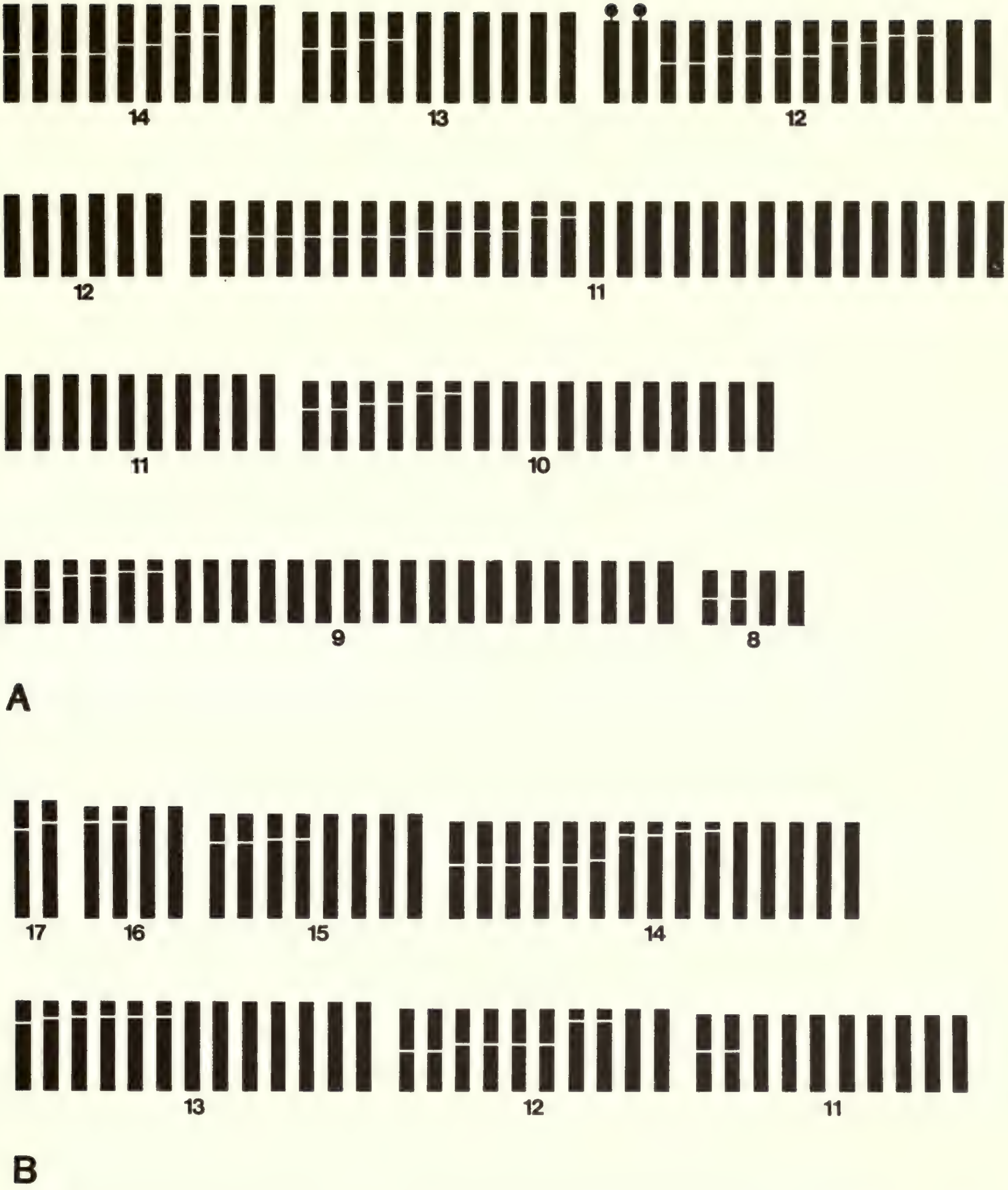

Fig. 46 Karyograms of *Blechnum*. **A**, *B. occidentale*, J11283 (4x). **B**, *B. fraxineum*, J10981 (2x). Each unit of length = 0·33 μm.

thinner towards the edge, unlike those of *B. occidentale* which are broad, very light brown in colour, and uniformly thin-walled. The triploid has light-coloured scales of intermediate shape and, whilst some of the scales have a central dark streak, others lack it.

Plants collected in Jamaica (under T4313–T4316, T4318) in the company of G. R. Proctor from the type population of *B. antillanum* Proctor were also found to be triploids with irregular chromosomal pairing (Walker, 1966*a*, 1973*b*). Two cells were analysed precisely and were found

Table 18 Number of chromosomes in each centromere position in *Blechnum fraxineum* (4*x*) and its assumed diploid parents, *B. fraxineum* (2*x*) and *B. 'unknown'* (2*x*). The centromere data for *B. 'unknown'* have been obtained by subtracting the figures in the second column from those in the first column. (For explanation of symbols see p. 152.)

	B. fraxineum (4*x*)	*B. fraxineum* (2*x*)	*B. 'unknown'* (2*x*)
M	4	2	2
m	16	12	4
sm	12	4	8
st	22	12	10
t	37	4	33
T	33	28	5
Totals	124	62	62

to have 16 bivalents plus 61 univalents in one instance, and 21 bivalents plus 51 univalents in the other. These results lie within the range of chromosome pairing shown by *B.* ×*caudatum* in Trinidad (Table 19). I am unable to find any distinguishing features, either in herbarium specimens or in plants grown side by side in cultivation, which would separate Jamaican *B. antillanum* from Trinidadian *B.* × *caudatum*, and must conclude that they represent the same taxon, being of hybrid origin from the same parental species. A morphologically similar plant from Belize was also found to be triploid with 2n = 93. *B.* × *caudatum* is widespread among the islands of the Caribbean and adjacent territory, and, because of its hybrid sterility, the implication is that it must have arisen independently in different areas and localities and also probably at different times. Once established, as a consequence of its stoloniferous habit this hybrid can rapidly build up large local populations which are similar in appearance to populations of normally reproducing gregarious species.

The evidence from karyotypes helps to confirm the deduction made on morphological grounds and on chromosome numbers that *B.* × *caudatum* is in fact the hybrid between tetraploid *B. occidentale* and diploid *B. fraxineum*. The karyograms of all three taxa are shown in Figs 46A, B & 47A, together with the summaries of centromere positions (Table 20). It will be noted that *B. occidentale* has an exceptionally large number of chromosomes having their centromeres at the median point M, and that these are distributed more or less evenly through the size classes of the chromosomes. In addition, two chromosomes are satellited. By contrast, diploid *B. fraxineum* has only a single pair of chromosomes with median point centromeres, and these belong to the smallest size class. No satellites are present. If the centromere classes are set out in tabular form (Table 20), and the half-number for each parental species is given in parentheses as representing the gametic complement, it will be seen that there is remarkable agreement in that the somatic complement of *B.* ×*caudatum* is the sum of the gametic

Table 19 Pairing at meiosis of the 93 chromosomes in *Blechnum* × *caudatum*.

Nos. of cells	No. of bivalents	No. of univalents
1	12	69
2	13	67
1	14	65
2	15	63
2	16	61
2	17	59
2	19	55
1	21	51
1	22	49

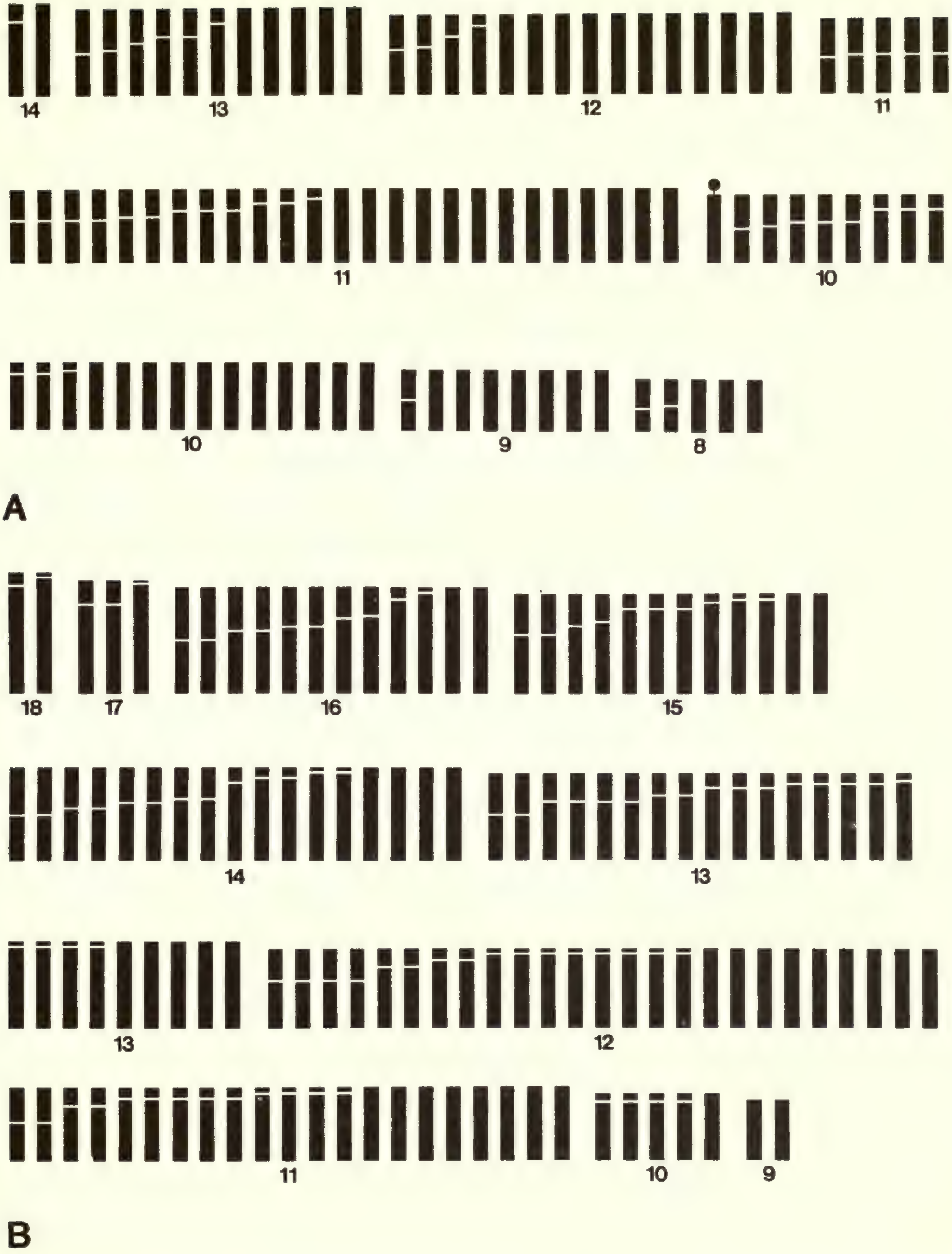
14
13
12
11
11
10
10
9
8
A
18
17
16
15
14
13
13
12
11
10
9
B

Fig. 47 Karyograms of *Blechnum*. **A**, *B. antillanum* (= × *caudatum*), T4136 (3x). **B**, *B. fraxineum*, NY6 (4x). Each unit of length = 0·33 μm.

Table 20 Number of chromosomes with each centromeric position in Blechnaceae. The numbers in brackets are gametic numbers. (See p. 152 for explanation of symbols.)

	Blechnum unilaterale (4*x*)	*B. occidentale* (4*x*)	*B.* × *caudatum* (3*x*)	*B. fraxineum* (2*x*)	*B. fraxineum* (4*x*)	*B. serrulatum* (2*x*)	*Salpichlaena volubile* (2*x*)
	Base number = 31					Base number = 36	Base number = 40
M	8	8(4)	5	2	4	2	2
m	14	20(10)	16	12(6)	16	6	8
sm	2	12(6)	8	4(2)	12	8	4
st	4	10(5)	11	12(6)	22	12	20
t	36	0(0)	2	4(2)	37	0	34
T	60	72 + 2* (36 + 1*)	50 + 1*	28(14)	33	42 + 2*	12
Total	124	124	93	62	124	72	80

* additional satellite chromosomes.

complements of *B. occidentale* and diploid *B. fraxineum*. No doubt there is a small element of chance in the agreement being so exact, but this example does illustrate the potential usefulness of karyotypic analysis in certain cases of suspected hybridity and in determining the possible parentage of a plant.

In *B.* × *caudatum*, as may be seen in Table 19, the amount of pairing of the chromosomes is variable, but in every case an appreciable number of bivalents ranging from 12 to 22 are formed. These bivalents may be the result either of autosyndesis amongst members of the sets of chromosomes contributed by *B. occidentale* or of allosyndesis between the appropriate chromosomes contributed by *B. occidentale* and *B. fraxineum*. This turns on whether *B. occidentale* is autoploid or allopolyploid in origin. Although the separation between peaks is not great the karyogram (Fig. 46A) is bimodal with two peaks, one occurring at 9 units of length (3·0 μm) and the other at 11 units (3·66 μm), thus indicating an allopolyploid nature. It follows that the pairing found in the hybrid *B.* ×*caudatum* is allosyndetic with some of the chromosomes of *B. fraxineum* having sufficient residual homologies with similar ones in *B. occidentale* to allow this to occur (Fig. 47). This is a somewhat similar situation to that found at the diploid level in the case of *Adiantum* ×*villosolucidum* (see p. 173).

Stolze (1981) has recognised the difficulties inherent in studies of some members of *Blechnum* in Guatemala, particularly in his interpretation of *B. fraxineum* which he recognises as being closely allied to *B. occidentale,* and states that the variations shown by it are infinite and not consistent. It is clear that here he is dealing with a complex rather than a single species, and indeed his illustration of '*B. fraxineum*' (Stolze, 1981: 107, fig. 13c) appears to be of *B.* × *caudatum*. Similarly, Murillo (1968) also takes a wide view of *B. fraxineum*. Thus, her fig. 133b appears to be of *B. fraxineum* in the narrow sense, whilst fig. 134b is typical of *B.* × *caudatum*. A comparison of the features of *B. occidentale, B.* × *caudatum,* and *B. fraxineum* is presented in Table 21 in the hope that this will go some way to clarifying the situation. However, it must be recognised that this group still poses enormous problems. At the present it is known that *B. occidentale* may hybridize freely with *B. unilaterale,* at least in Jamaica (Walker, 1966*a*, 1973*b*) and no doubt elsewhere where the two species occur together, as well as with diploid *B. fraxineum*, as reported here. There is the distinct possibility of other hybrids occurring, although not yet confirmed, which may be blurring specific boundaries even further, such as *B. fraxineum*(2x) × *B. fraxineum*(4x), *B. occidentale* × *B. fraxineum*(4x), *B. unilaterale* × *B. fraxineum*(2x) and *B. unilaterale* × *B. fraxineum*(4x). Living material of each of the basic species is in cultivation at Newcastle and it is hoped to synthesise all these hybrids and compare their morphological and cytological features. Until this is done and the specimens compared with

Table 21 Comparison of *Blechnum occidentale, B. fraxineum* (2*x* cytotype), and *B.* × *caudatum.*

Characters	*B. occidentale*	*B.* × *caudatum*	*B. fraxineum*
1. Terminal pinna	merges with lateral pinnae; *c.* ½ × length of longest lateral	abrupt; same or slightly longer than longest lateral	abrupt, petiolate; 1½–2 × length of longest lateral
2. No. of pinnae pairs	12–20+	6–12	1–3
3. Base of pinnae	cordate	not cordate	not cordate
4. Glandular hairs	present (in Trinidad material)	sparse	virtually absent
5. Scales	broad, light brown, concolourous	intermediate, dark centre sometimes present	narrow, dark brown
6. Spores	viable	non-viable (see text)	viable
7. Cytology	sexual tetraploid meiosis regular	sterile triploid meiosis irregular	sexual diploid meiosis regular

wild-collected material, it is unwise to pass sweeping taxonomic judgements in this group. It may be noted in passing that, unlike the situation in most other genera, sterile interspecific hybrids are not always easy to detect on herbarium material using the presence of abortive spores as a criterion. The spores in this complex tend to be more or less colourless and the abortive ones do not seem to collapse to the extent found in many other fern hybrids. The result is that the abortive spores are not immediately obvious in a quick microscopic examination.

Despite the complexity uncovered above in Trinidad, and the potential for further interspecific hybridization, it is clear that as far as the *B. occidentale* complex is concerned only the tip of the iceberg has been so far exposed. That this complexity is much greater can be indicated by a couple of examples. In the first instance, Jarrett, Manton & Roy (1968) confirmed the presence of tetraploid *B. occidentale* on Galapagos. However, they also showed that a triploid plant with irregular meiosis was also present. The morphology of this triploid is very close to that of typical *B. occidentale* and quite unlike that of *B.* × *caudatum*, suggesting the presence of yet another hybrid combination in this complex and yet another diploid species. In the second example *B. occidentale* itself is genetically variable. Stolze (1981) recognises two varieties in Guatemala, var. *occidentale* and var. *pubirhachis* Rosenst., which also correlate with altitude in that the glabrous var. *occidentale* is found at 1000 m and below, whilst var. *pubirhachis* with glandular hairs present on the rachis occurs from 1200 to 2700 m. He quotes Lellinger as confirming a similar situation in Costa Rica and Panama. Whilst both glabrous and non-glabrous forms occur in Jamaica, all specimens from Trinidad are glandular to varying degrees and all were gathered well below 1000 m (at 500 m or less). Clearly, in Trinidad the pattern of events is quite different from that of the mainland at least in this respect.

The remaining member of the complex to be considered is *B. unilaterale*. This is a sexual tetraploid (Fig. 45C) as has also been found to be the case in Jamaica (Walker, 1966*a*) and the Galapagos (Jarrett, Manton & Roy, 1968). Its karyotype (Fig. 48A and Table 20) shares with *B. occidentale* the somewhat unusual feature of relatively many (8) chromosomes having centromeres at the median point M, but it lacks satellites. Another unusual feature is the small range and average size of the chromosomes (from 2·0 to 3·33 μm).

The only other commonly occurring species of *Blechnum* in Trinidad is *B. serrulatum*, which is based on the entirely different chromosome number of x = 36. It is also unique in being the only member of the genus on the island which is a plant of swamps and savannas. Features of its ecological behaviour and anatomy have been discussed in Jermy (1985). One plant was cytologically examined from Icacos Point in the south west of the island, where this species forms dense stands at the edge of the swamp near the sea and in which *Acrostichum danaefolium* was abundant. It was diploid with n = 36 and was reported (Walker, 1966*a*) under the name of *B. indicum* Burman f., as confirmation of the count obtained from a Jamaican plant from a savanna habitat. However, this name is applicable to Asiatic material and is not appropriate for American specimens which should be known as *B. serrulatum*. A further count from a plant sent by A. C. Jermy to Newcastle from Aripo Savanna in the centre of Trinidad gave a somatic count of 2n = 72. The roots of this species have proved to be very troublesome cytological subjects in that they possess very few active meristematic cells in proportion to older matured cells. As a consequence fixations had to be made on numerous occasions before good preparations were obtained (Fig. 45D). The resultant karyogram and centromeric analysis are presented in Fig. 48B and Table 20. Whilst the basic chromosome number is very different from that of the *Blechnum occidentale*–*B. fraxineum* complex (36 versus 31) it is not possible at this stage to make any valid comparison between the two groups in view of the wide range of karyotypes shown by various members of the complex, and this aspect must await the results of analysis of many more species. It may be worthwhile, however, to draw attention to the fact that the satellites occur on the smallest chromosomes of *B. serrulatum*, as compared with the situation in *B. occidentale* where they occur on two of the larger chromosomes.

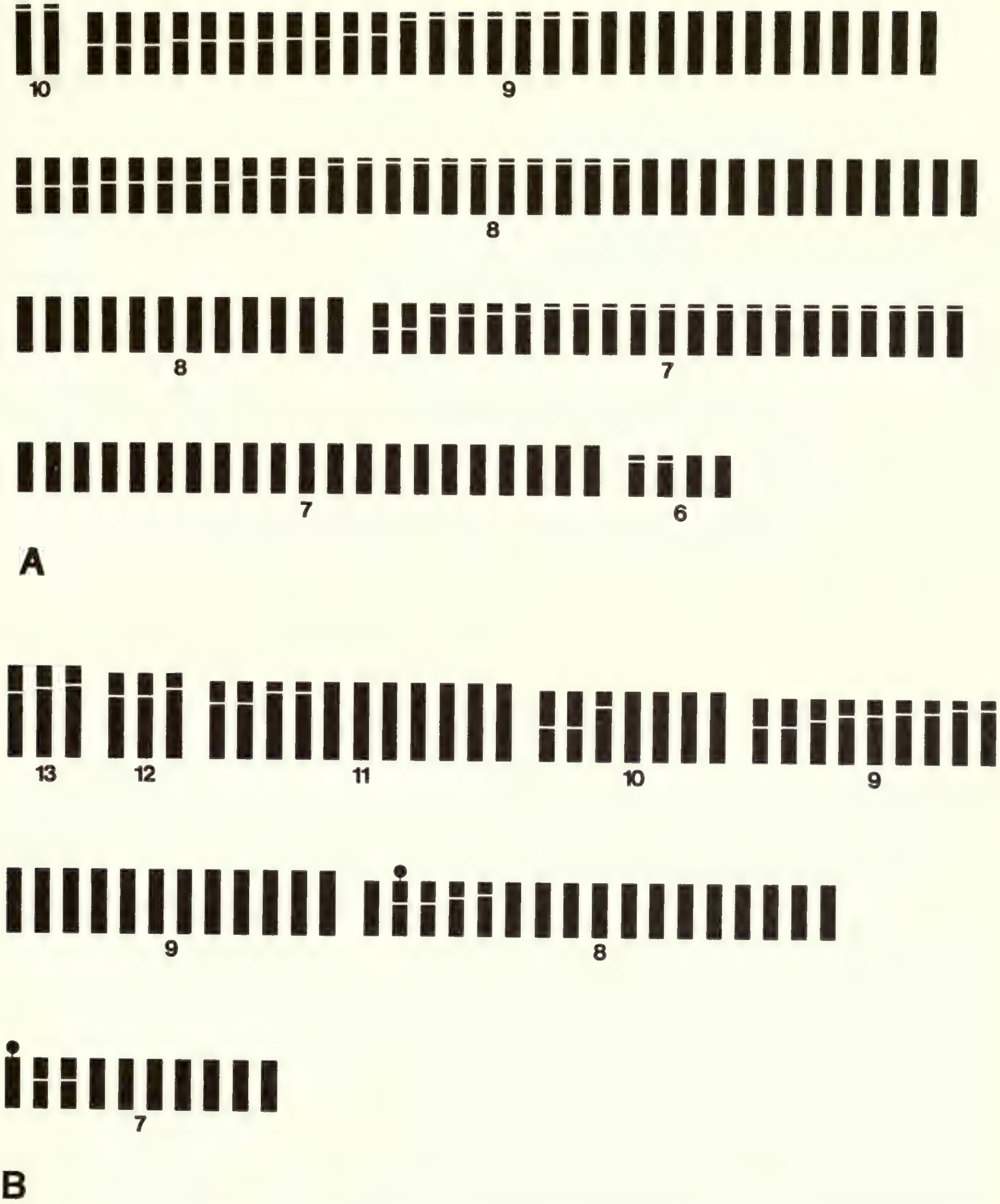

Fig. 48 Karyograms of *Blechnum*. **A**, *B. unilaterale*, T4439 (4x). **B**, *B. serrulatum*, J11215 (2x). Each unit of length = 0·33 μm.

2. Salpichlaena J. Smith

Salpichlaena is represented by a single species *S. volubilis*, which occurs in Central and South America with an extension via Trinidad and Tobago, together with a few islands of the Lesser Antilles, into the West Indies. Whilst a small number of species of *Blechnum*, such as *B. fragile* (Liebm.) Morton & Lellinger and *B. ensiforme* (Liebm.) C.Chr., climb on trees often quite high above ground level, they achieve this by means of scandent rhizomes. *Salpichlaena*, however, represents a unique case in the family Blechnaceae of a climbing fern in which the creeping rhizome is wholly terrestrial, and it is the fronds of indeterminate growth which climb over shrubs and trees and often reach a considerable length. Superficially, the fronds bear some resemblance to those of a large-leaved species of *Lygodium*, such as *L. circinatum* (Burman f.) Swartz. However, not only are the fertile areas very different, but the pinnae differ in their basic construction. In *Lygodium* the rachis undergoes successive unequal dichotomies, the smaller branch (the primary rachis branch) being very short and terminating in a dormant apical bud. These small branches produce paired secondary rachis branches bearing leaflets (for details see Holttum, 1954, 1959). In sharp contrast the rachis of *Salpichlaena* grows indefinitely and produces true lateral pinnae. Holttum (1954: 53) states that no ferns other than *Lygodium* have a twining rachis. However, this is the case also with *Salpichlaena*, enabling the fronds to be very efficient climbers rather than mere scramblers.

Apart from the climbing habit of the frond, in almost all other respects *Salpichlaena* is clearly blechnoid, e.g. in spore morphology, sporangial structure, soral characteristics, frond architecture, anatomy, and in the typical red colouration of the young fronds. The fronds first produced by young plants are simple and erect, with prominent stipes up to 40 cm long (Fig. 50A), and could easily be mistaken for sterile plants of *Blechnum lanceola* Sw. It is only as the plants mature that the typical climbing pinnate fronds are produced (Fig. 50B). This genus has proved to be difficult to grow satisfactorily in cultivation. The spores appear to have only a short viability period, and transplanted specimens tend to die after a few months or a year or two or, even if they survive to maturity, they tend not to flourish or to be anything like as vigorous as they are in the wild.

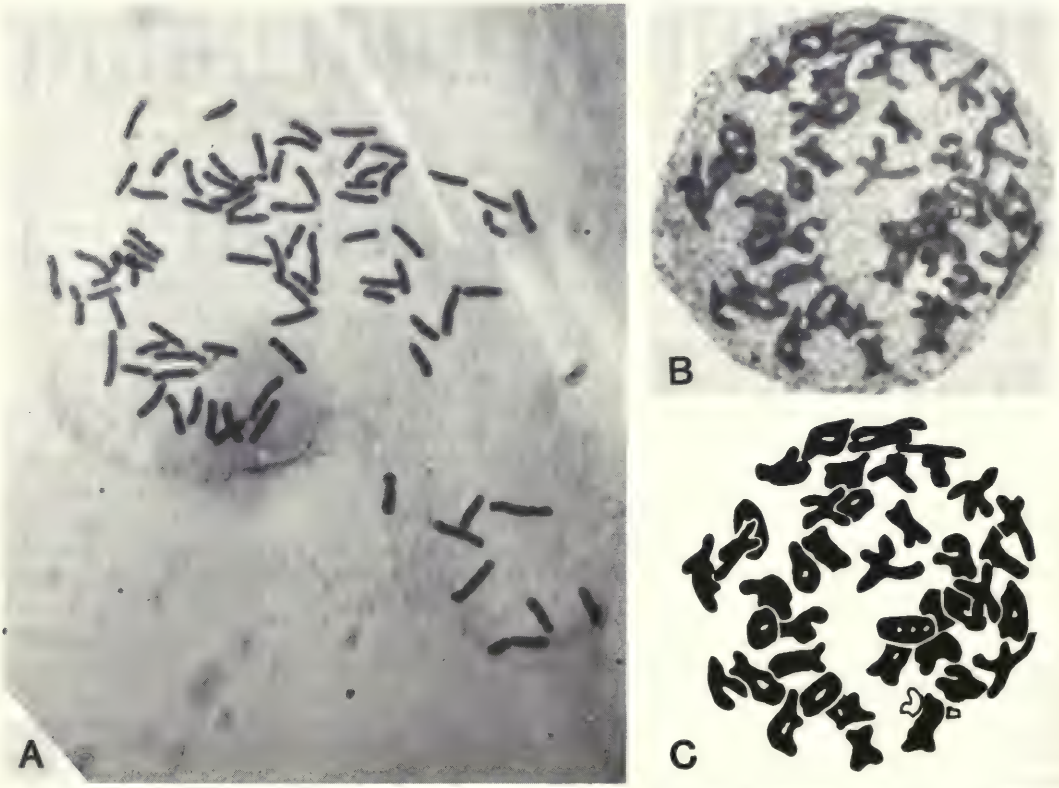

Fig. 49 *Salpichlaena volubilis.* **A**, T10915, mitosis, 2n = 80, × 1000. **B**, T10831, meiosis, × 1000. **C**, explanatory diagram of B, 40 bivalents, × 1000.

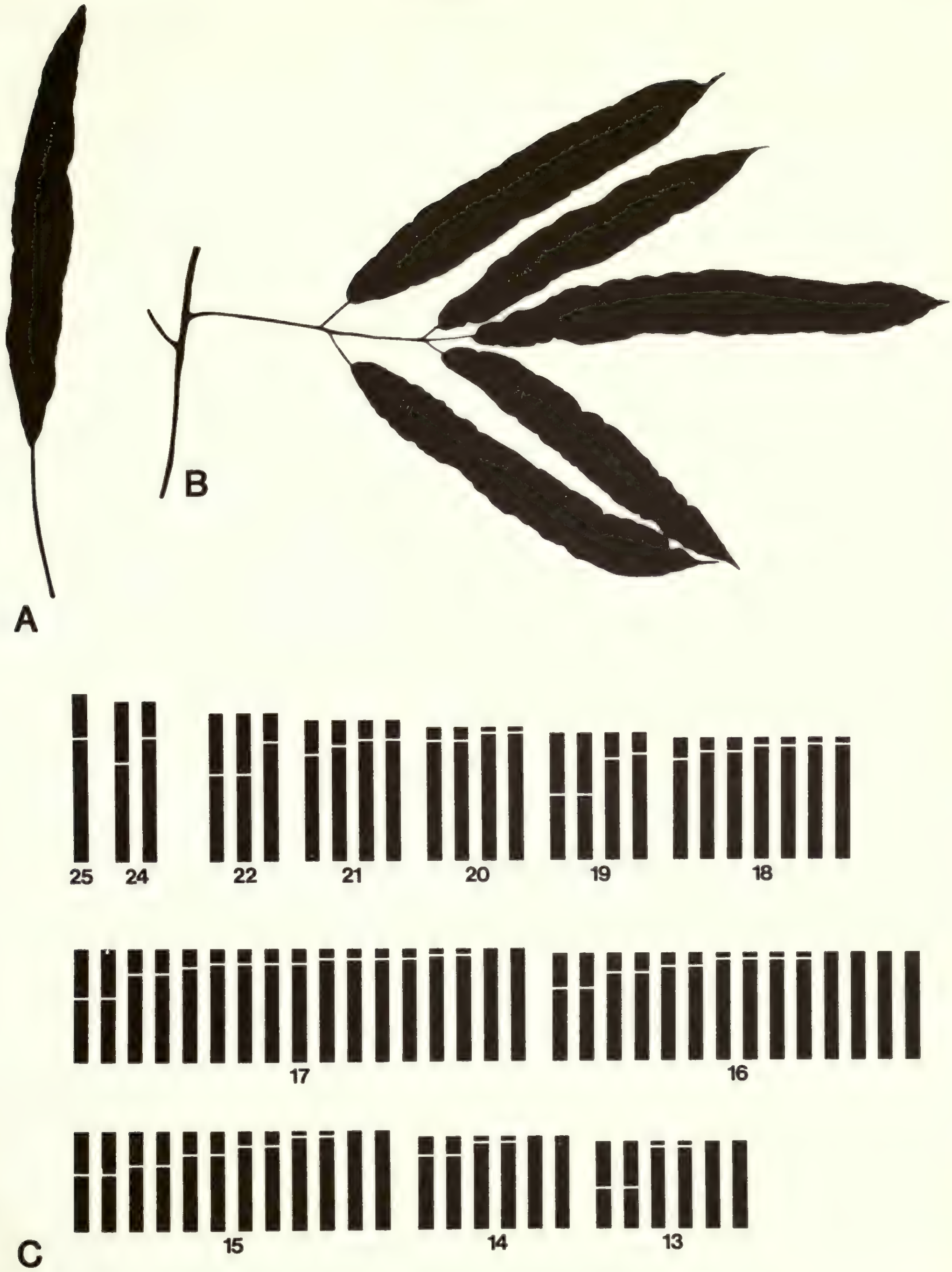
A
B
25
24
22
21
20
19
18
17
16
15
14
13
C

Fig. 50 *Salpichlaena volubilis*. **A**, silhouette of entire young frond, × 1/2. **B**, silhouette of a sterile pinna of a mature frond, × 1/2. **C**, karyogram. Each unit of length = 0·33 μm.

Meiosis was examined from two plants from Trinidad (Walker 1973*b**) and, despite the somewhat sticky chromosomes, several cells clearly showed 40 bivalents (Fig. 49B & C). Root tips from a further two specimens yielded actively dividing nuclei and they showed $2n = 80$ unequivocably (Fig. 49A), the species thus being a sexual diploid based on $x = 40$. An examination of the karyotype (Fig. 50C) of *Salpichlaena* shows that the chromosomes are outstandingly different from those of the other members of Blechnaceae examined here. They are consistently large with a wide range in length (from 4·33 to 8·33 μm), and are immediately recognizable by this character alone. That this is not merely due to poor contraction of the somatic chromosomes in the cells examined may be seen from a comparison of meiosis in *Salpichlaena* and *B. fraxineum* (Figs 49B & 44B), in which the large size of the bivalents in *Salpichlaena* is immediately obvious. A further noteworthy feature of the somatic chromosomes is seen in the relatively small number in which the centromeres are either genuinely terminal or so close as to be indistinguishable (Table 20).

The chromosome number of *Salpichlaena*, based on $x = 40$, is at the extreme top end of the aneuploid series of chromosome numbers found elsewhere in the whole family Blechnaceae, running from $x = 28$ to $x = 37$. Whilst the blechnoid nature of the plant is not in doubt (as has been indicated by some authors adhering to Kaulfuss' name of *Blechnum volubile*) it is nevertheless strongly isolated from other members chromosomally, genetically, and in its climbing habit, justifying its generic recognition. In dealing with an aneuploid series it is always difficult to decide which is an original number or which numbers represent loss or gain. The strongly asymmetric histogram of chromosome lengths of *Salpichlaena* suggests that its basic chromosome number of 40 is a derived one. In view of the somewhat specialized nature of *Salpichlaena* and the possession of a chromosome number at the top end of the series, the suggestion is that the unique number of 40 in this family has arisen from some lower original number.

General discussion

A total of 155 taxa/cytotypes of the ferns of Trinidad have been investigated cytologically, many of the results being new records. As in all fern floras that have been intensively sampled to a greater or lesser degree, hybrids have been shown to be commonplace, occurring in 15 different interspecific combinations and thus forming 10% of the total. Twenty-one hybrid combinations had been found in the fern flora of Jamaica (Walker, 1966*a*, 1973*b*), where they constituted 7·5% of the total number of taxa investigated. Of the combined total of 36 hybrid combinations, only one, namely *Blechnum* × *caudatum* (syn.: *B.* × *antillanum*), is common to the two islands. As regards the Trinidad hybrids, an analysis of their ploidies shows that the overwhelming majority, eight out of 11 (omitting the filmy fern hybrids whose true ploidy is uncertain and the cytologically uninvestigated *Lygodium* cross) are triploid, one is diploid, one is tetraploid, and one is pentaploid.

In a number of cases the hybrids are quite clearly products of crossing between members of closely knit species-complexes, such as those centred on *Blechnum occidentale, Gleichenia bifida,* and *Tectaria incisa*. In other cases they represent chance crossing between species which are not obviously members of large complexes, such as the hybrid '*Feea osmundoides*' and *Sphaerocionium* × *tucuchense*.

Fern hybrids of temperate regions tend to have a relatively clear-cut pattern of cytological behaviour in that their chromosomes predominantly associate in terms of whole, or approximately whole, genomes. The triploid hybrid *Asplenium* × *ticinense* D. Meyer with its 36 bivalents + 36 univalents at meiosis is typical of such behaviour. Indeed, this pattern is so commonplace that fern cytological literature is replete with formulae such as, n II's + nI's or nII's + 2nI's. This more or less rigid pattern to which major deviations are the exception rather than the rule in the Northern Hemisphere is certainly not one which is commonplace in the tropics, and, of the combined Jamaican and Trinidadian hybrids, only about eight, that is less than a quarter of the total, tend to follow this pattern – the large majority having a meiosis in which the chromosomes do not associate regularly in combinations of approximately whole genomes. Furthermore, the actual number of bivalents, univalents, etc., vary from cell to cell (e.g. Tables 7 and 19). This type of behaviour is not peculiar to the Caribbean but is the more normal pattern in fern floras in many tropical countries (Walker, unpub.). Judging by the wide geographical range of many of the members of species complexes in, for example, *Asplenium, Dryopteris,* and *Polypodium*, temperate ferns have tended to keep their homologies intact for considerable lengths of time. The same does not appear to be true to the same extent in tropical ferns. In some cases, where cells showing a genomic pattern of pairing may be encountered, other cells in the same plant may fall far short of this, e.g. in *Adiantum* × *villosolucidum* (Table 7) and in *Tectaria* × *bulbifera*, where, although 40 bivalents + 40 univalents have been found, other cells show virtually complete failure of pairing of the chromosomes. Rapid loss of homologies at the diploid level allows speciation by genetic means as a result of developing chromosomal isolation, and there is a reasonable inference to be made that this has been a potent factor, for example, in South American members of *Adiantum, Elaphoglossum,* etc.

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* Three collection numbers were quoted as having been cytologically examined. Only two (*Walker* T6413 and T10831) were in fact examined, specimen T6713 being quoted in error.

Aneuploidy in ferns usually occurs at the generic, subgeneric, or similar level. In a number of cases somewhat random loss or gain of chromosomes has taken place, but these are usually in ferns which are clearly highly polyploid in the first instance whether by virtue of having high base numbers, e.g. *Ophioglossum, Schizaea*, etc., or by more immediate polyploidy, such as in the octoploids and decaploids of *Adiantum*. However, *Adiantum* has also been shown to deviate at the diploid and tetraploid levels from strict multiples of 29 or 30 (Bidin, 1980; Walker, present comm.) in root tip cells. It would be interesting to take such an aneuploid plant and subject it to a thorough analysis to see if all the somatic cells constantly deviated from the norm and to study the effect, if any, on meiosis and spore production.

The overall percentage of polyploidy at 50% in Trinidad is appreciably lower than the 60% level attained in Jamaica (Walker, 1966*a*, 1973*b*) and this figure is further somewhat depressed if one removes the four certainly naturalized species which are all tetraploid, namely *Amphineuron opulentum* (Kaulf.) Holttum, *Christella dentata* (Forsskal) Brownsey & Jermy, *Macrothelypteris torresiana* (Gaudich) Ching, and *Pteris vittata* L. The reasons for such a difference may be even more complex than usual in that Trinidad's mountains are low relative to those of Jamaica, and hence a whole sector of vegetation based on altitude tends to be missing. Such a wide range of stratification is considered to be important in promoting polyploidy when coupled with unstable conditions over geological time (Walker, 1984). Additionally, there is the question of the sources of the ferns. Many species are shared in common between Jamaica and Trinidad, but there is a large predominantly South American element in the Trinidad flora, which is hardly surprising in view of the separation of the island and the mainland at the present time by only a very narrow strait and their actual conjoining in the recent past. Similarly, Jamaica has a significant Central American element in addition to the shared South American one. Such an interplay of factors makes analysis difficult as to the causes of the differences between Jamaica and Trinidad. However, if one considers Trinidad as geographically a small fragment of South America, the figures would suggest that polyploidy in the continent may be appreciably lower than in say Sri Lanka or West Africa for which figures of *c.* 60% have been obtained (Manton & Sledge, 1954; Manton & Vida, 1968) and more nearly approach those of Malaya (Manton, 1954) and Sarawak (Walker, unpub.) which are approximately 40%.

Evidence from morphology, cytology, and a study of hybrids suggests that the vast majority of Trinidadian polyploids are alloploid in nature. However, the tetraploid form of *Bolbitis hemiotis* is probably an exception, and less certainly the same may be true of the hyper-octoploid cytotype of *Adiantum pulverulentum*.

Apart from the cytological evidence, spore and stomatal measurements may provide a reliable means of distinguishing between different cytotypes of the same species in herbarium material, though experience has indicated that these must be used with caution and only after first testing against cytologically authenticated material. This may prove to be particularly useful in the case of small plants forming populations of large numbers of individuals where the species has been shown to be cytologically heterogeneous, e.g. *Xiphopteris serrulata*. By contrast some cytotypes show little or no differences in their measurements, such as in the diploid and tetraploid forms of *Polypodium triseriale* from Jamaica and Trinidad.

As in Jamaica agamospory is apparently very infrequent in Trinidad, having been detected in only three species, comprising some 2% of the sample investigated. The triploid *Anemia pastinacaria* with its two types of behaviour of meiosis in the spore mother cells undoubtedly conforms to the 'Manton scheme' of sporogenesis, the spore-mother cells (smc) showing all bivalents eventually producing spores with the unreduced chromosome number which will be viable and reproduce the plant, whilst the smcs with a mixture of bivalents and univalents produce mis-shapen non-viable spores. The other two agamosporous species, namely *Asplenium macilentum* and *Xiphopteris serrulata*, were also found to be agamosporous in Jamaica. These produce only univalents at meiosis, an earlier statement (Walker, 1966*a*) that some cells of *Xiphopteris* produce bivalents appears to have been based on a misidentified preparation. This behaviour suggests that here the 'Braithwaite scheme' of sporogenesis is operating. The figures for agamospory are low for both Trinidad (2%) and Jamaica (3%), when compared with those of fern floras of North America and Japan with *c.* 9% and 18% respectively (Walker, 1979). The reason for the high-figures for the latter countries lies in the presence there of large numbers of species in genera which themselves form an appreciable percentage of the total flora and which are very prone to agamospory e.g. *Dryopteris, Pellaea, Polystichum, Pteris,* etc.

Finally, the karyotyping has been carried out in the hope of accumulating data which may be of use in determining evolutionary trends and enlarging our knowledge. Even with the limited amount of data which has been accumulated it is evident that the technique is useful and has also allowed deductions to be made in some cases as to the alloploid or autoploid nature of individuals. Differences also appear to exist between representatives of different genera, e.g. *Blechnum* and *Polypodium*. However, the method should not be pushed too far and it is clear that it would be exceedingly difficult, if not impossible, to trace such events as individual translocations, unless these were phenomenally large.

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Cytotaxonomic studies of the ferns of Trinidad

3. Descriptions of new species and hybrids and a new combination

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Synopsis

As a result of the extensive collecting of ferns by the authors in Trinidad during 1963, 1966, and 1974 and a comprehensive cytological survey by T. G. Walker (part 2 of this work), five new species and nine new hybrids have been elucidated and are described. One new combination is made.

Introduction

This paper describes the new species and hybrids that have been collected by the authors in Trinidad, 1963–74, and their relationships further elucidated in the subsequent cytological studies by T. G. Walker. These latter results have been discussed by Walker (part 2 of this work) who also describes there the morphological characters of the hybrids and their putative parents. These discussions, therefore, are not repeated in detail in the present paper.

Bull. Br. Mus. nat. Hist. (Bot.) **13** (2): 251–276 Issued 30 May 1985

New species and hybrids

1. Lygodium ×fayae Jermy and T. Walker, hybrida nova

[*L. micans* Sturm × *L. venustum* Swartz] (Figs 1B & C, 2)

Planta sterilitate vigoreque hybrido distinguibilis et maximam partem inter *Lygodium micans* Sturm et *L. venustum* Swartz intermedia. A *L. micanti* (et *L. volubili* Swartz) costulis laminaque pulverulentis, sorophoro breviore, foliorum et sterilium et fertilium segmentis infimis pinnarum basi distincte lobatis vel pinnulis ovalibus differt. A *L. venusto* sorophoris longis linearibus, in quoque usque ad 30 soros, et pinnis longioribus lineari-lanceolatis distinguitur.

A vigorous plant, scrambling, typical of the genus. Rachis pinkish-brown, sparsely covered with ± adpressed short hairs; arrested bud and secondary rachis pubescent, hairs less adpressed; *pinna-branch* pinnate; *fertile pinna-segments* stalked, 6–7 pairs, alternate, 85–110 × 17–20 mm, linear with an acute apex or lanceolate, the lower ones auricled, lowermost segments deeply lobed, or with sessile or shortly stalked rounded or oval pinnules. *Sporangia* on elongate or linear marginal lobes (sorophores); spores abortive.

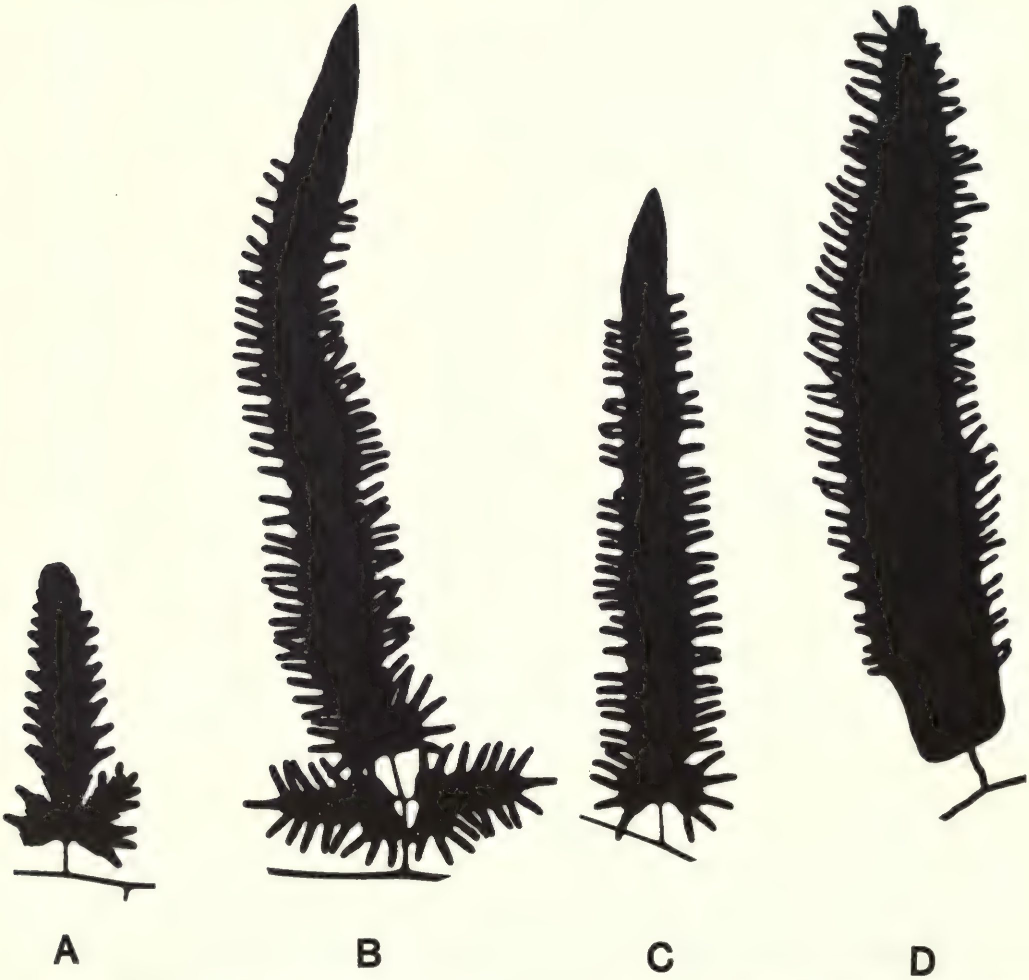


Fig. 1 Silhouettes of fertile pinnules of *Lygodium*. A, *L. venustum, T. G. Walker* T6013 (BM). B & C, *L. × fayae, T. G. Walker* T6960 (BM – holotype). D, *L. micans T. G. Walker* T6144 (BM). All from Trinidad. Natural size.

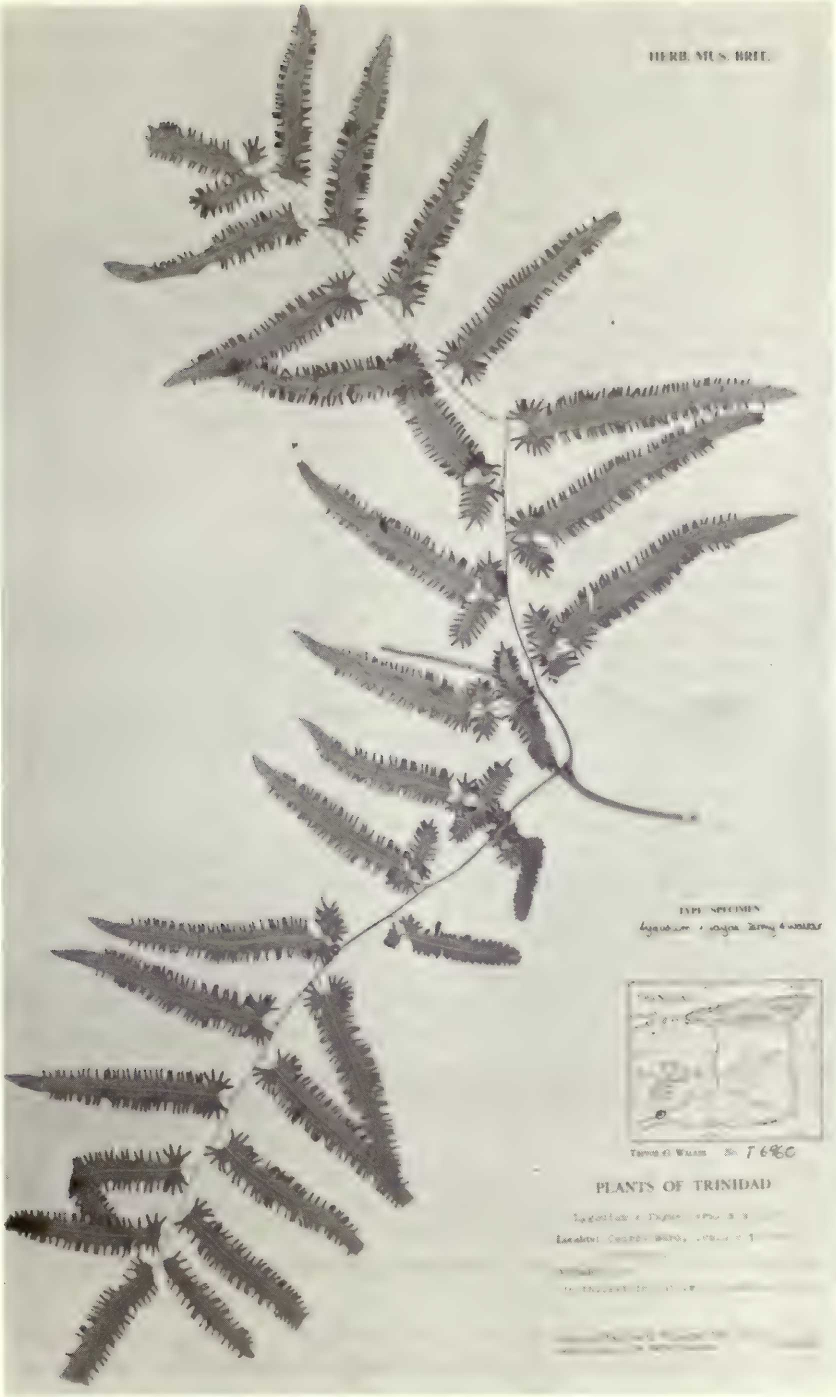

HERB. MUS. BRIT.
TYPE SPECIMEN
PLANTS OF TRINIDAD

Fig. 2 Holotype specimen of *Lygodium ×fayae* Jermy & T. Walker (BM).

Type: TRINIDAD, Cedros Ward, Irois, *c.* 0·5 km from sea, in thicket in cut-over secondary forest, 13 August 1963, *T. G. Walker* T6960 (BM – holotype; NY, TRIN-isotypes).

Paratypes: TRINIDAD, Arima Ward, 9 km N of Eastern Main Road, on Guanapo Heights Road, 160 m alt., trackside in secondary forest, 22 July 1976, *Barnard, Jones & Crane* 229 (BM, RDG). La Brea Ward, Guapo on sea shore climbing amongs shrubs, 13 May 1920, *W. E. Broadway* 7927 (BM); sine loco et dato, *I. V. Thompson* s.n. (BM).

A sterile plant of this tentative parentage was described from Guayaguayare by Dr Alice Fay (Fay, 1973: 165, fig. 2). This plant is named in recognition of her extensive collecting of ferns whilst at the University of the West Indies, St Augustine.

Although the cytology of this hybrid has not been examined, Walker (1985) discusses its morphology (Table 4). Its hybrid vigour is distinctive at any time. It is best distinguished from *Lygodium venustum* by the longer parallel sided sorophores (each with *c.* 30 sori); in the latter species the sorophore is rounded and constricted at its base and there are 8–10 sori in each. From *L. micans* (or *L. volubile*) it is more difficult to separate, but the fertile pinna-segments are shorter and more rounded, and in both fertile and sterile leaves at least the lower pinna segments are usually distinctly lobed or even pinnate at the base, and are hairy on the costules and lamina surface.

2. **Adiantum × variopinnatum** Jermy & T. Walker, **hybrida nova**
[*A. latifolium* Lam. × *A. petiolatum* Desv.] (Fig. 3)

Hybrida sterilis vix alio modo ab *Adianto petiolato* Desv. distincta, sed e rhizomate breviter repenti unum saltem folium bipinnatum pinna singulari vel etiam pare basali tripinnato emittens. Eadem propietate a parente altero, *A. latifolio* Lam., cuius folia pinnata 2–3(<6) iterum divisa, et pinnulis rhombeis (non ut in *A. latifolio* e basi gradatim angustatis) manifestius differt.

Rhizome shortly creeping, covered with narrow-triangular, almost acicular, entire brown-metallic scales *c.* 1·5 mm long. *Fronds c.* 60 cm, ± erect or slightly arching, ± closely together; *stipe* shiny, black with a tinge of red-brown, glabrous below but with scant filiform golden-brown scales of 5–10 cells in the abaxial groove above; *lamina* deep green above, glaucous beneath, 26 × 16 cm, generally lanceolate in outline and pinnate, occasionally one, or more rarely both the lowermost pinnae again pinnate and broadly ovate-lanceolate in outline; *lower pinnae* 64 × 30 mm, asymmetrically triangular, base truncate, apex acute, midrib median, with 5 mm petiole; *upper pinnae c.* 50 × 20 mm decreasing to 18 × 6 mm, dimidiate, squarrose at the base on the acroscopic side, sharply cuneate on the basiscopic side, linear, tapering to acute apex in upper half, shortly petiolate; *terminal pinna* and *pinnules* when present similar to upper pinnae; rachis purplish-brown furfuraceous with gingery-brown filiform scales. *Sori* along entire margin, interrupted; *indusium* linear, semi-elliptic or occasionally lunulate; *spores* abortive.

Type: TRINIDAD, Tacarigua Ward, Tunapuna, two miles up Caura Road near river, *c.* 60 m alt., on sides of gully in secondary forest, 6 July 1963, *A. C. Jermy & T. G. Walker* J2070 (cytol. ref. no. T6123) (BM – holotype; TRIN-isotype).

Paratypes: TRINIDAD, Tacarigua Ward, same locality and date, *A. C. Jermy & T. G. Walker* 2068 (cytol. ref. no. T6122) (TRIN); Tunapuna, valley above St John's, 60 m alt., on track bank in clay soil, 25 October 1974, *A. C. Jermy* 10993 (NY). Diego Martin Ward, Mount Catherine, SE. slopes, 20 m alt., in loamy forest soil, 30 October 1974, *A. C. Jermy* 11061 (herb. Walker).

All the paratypes have been cytologically checked showing 90 chromosomes (triploid) and an irregular meiosis. The cytology and variable morphology is discussed and tabulated in Walker (1985: figs 11C, D, and E and table 6).

This hybrid is difficult to distinguish from *Adiantum petiolatum* if fully formed sporangia with abortive spores are lacking. There is usually one frond on the relatively short-creeping rhizome which is bipinnate with a single or pair of pinnate pinnae at the base. From the other parent, *A.*

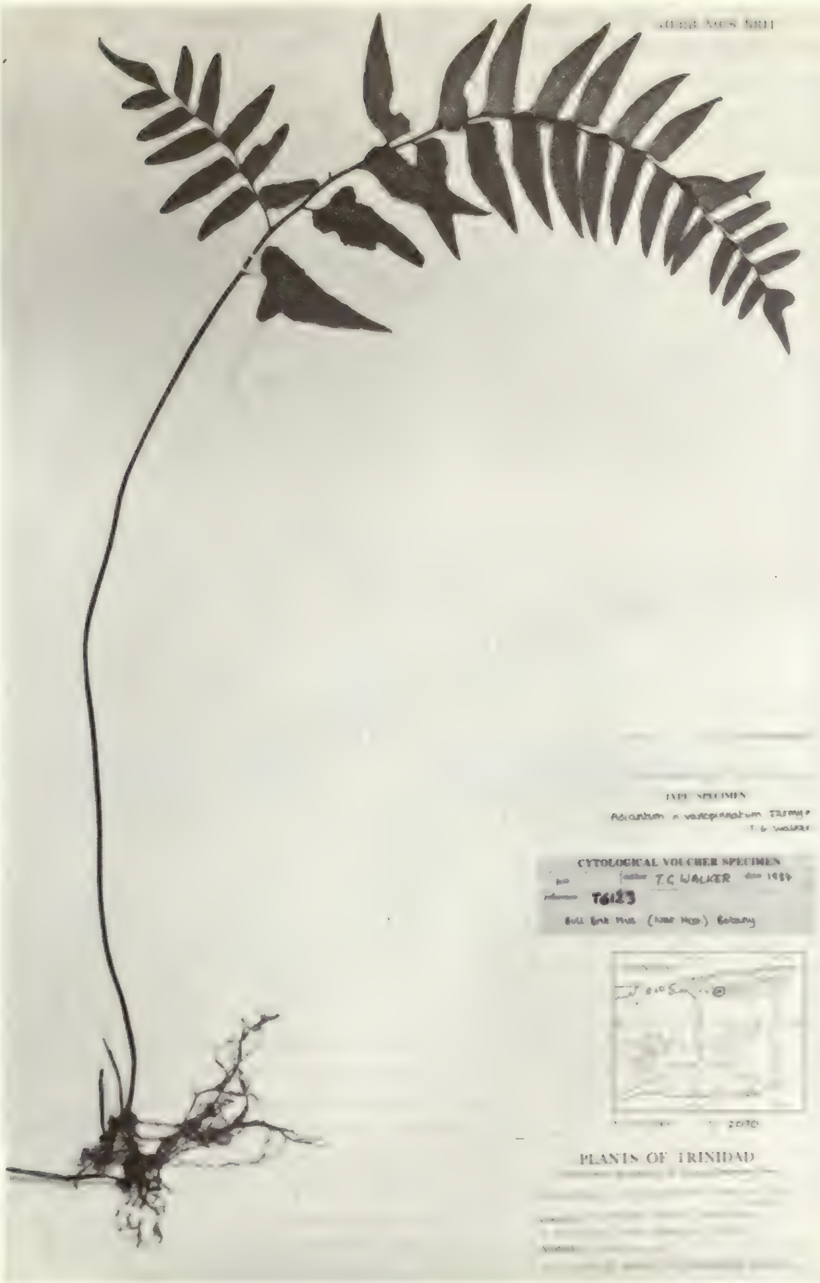

TYPE SPECIMEN
CYTOLOGICAL VOUCHER SPECIMEN
T.G. WALKER
T6123
PLANTS OF TRINIDAD

Fig. 3 Holotype specimen of *Adiantum* ×*variopinnatum* Jermy & T. Walker (BM).

latifolium, it is easier to distinguish as the latter has usually 2 or 3 (<6) compound lower pinnae, which are pinnate and more or less equal to the remaining pinnate portion of the frond. The ultimate segments (pinnules) are more tapered from the base and appear triangular, whereas in *A.* ×*variopinnatum* the ultimate segments are parallel sided in the lower half.

3. **Adiantum** × **villosolucidum** Jermy and T. Walker, **hybrida nova**
[*A. lucidum* (Cav.) Swartz × *A. villosum* L.] (Fig. 4)

Hybrida inter parentes, *Adiantum lucidum* (Cav.) Swartz et *A. villosum* L. interposita. Ab *A. lucido* paribus 1–3 pinnarum compositarum basin versus frondis, segmentis ultimis brevioribus minus succulentis et petiolo laevigato distinguitur. Ab *A. villoso* pinnis compositis paucioribus, segmentis ultimis crassis vix aggregatis differt.

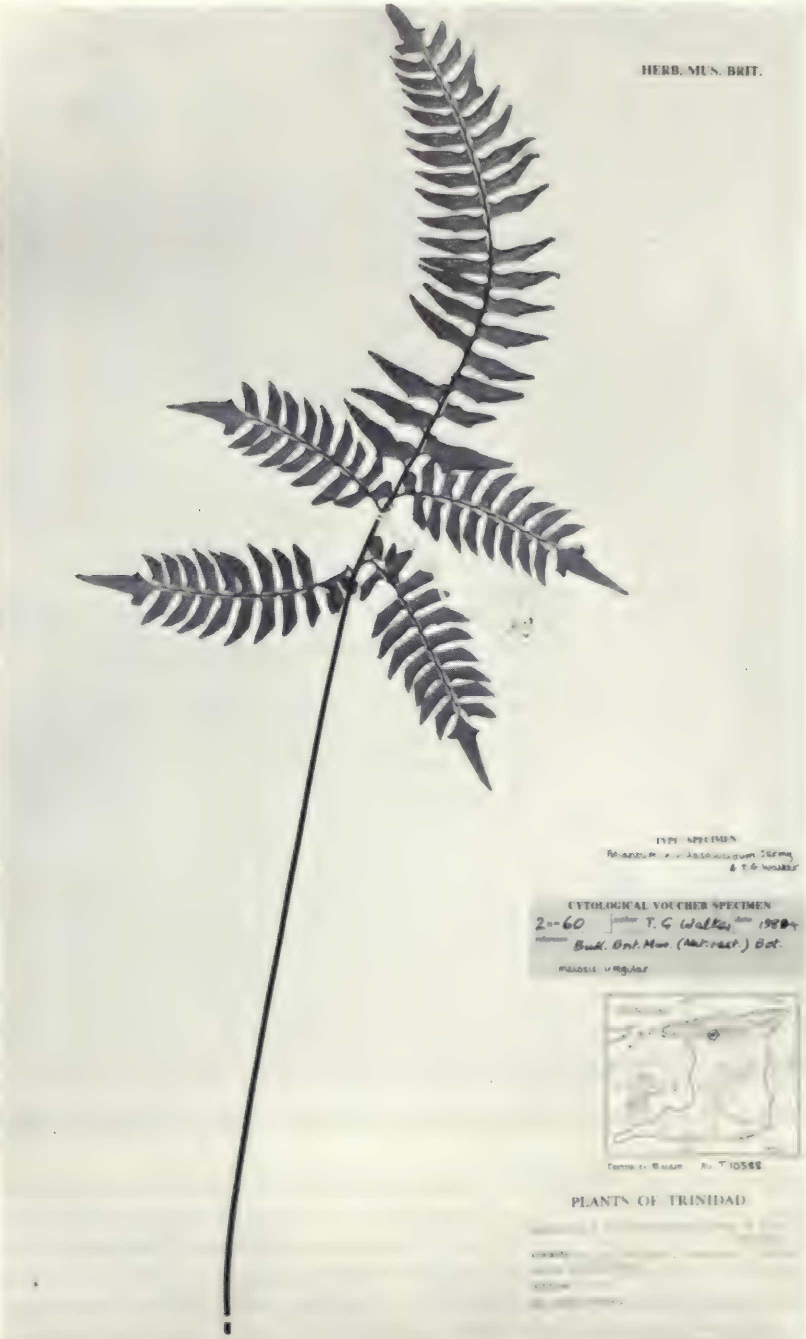

HERB. MUS. BRIT.
TYPE SPECIMEN
CYTOLOGICAL VOUCHER SPECIMEN
2n=60
T. G. Walker
PLANTS OF TRINIDAD

Fig. 4 Holotype specimen of *Adiantum* × *villosolucidum* Jermy & T. Walker (BM).

Rhizome short-creeping, clothed in narrow triangular metallic brown scales 1·5–2·0 mm long. *Fronds* at maturity 45–55 cm long, erect, few, clustered together at rhizome apex; *stipe c.* 30 cm, shiny, black with a tinge of red, glabrous below soon becoming ± densely covered above with filiform or arachnoid minute, gingery-brown scales; *lamina c.* 25 × 20 cm, herbaceous, dark green on both surfaces, bipinnate, with 2 or 3 compound pinnae; *pinnae* 100–110 × 30–40 mm, lanceolate, pinnate with a terminal pinnule; *pinnules* (ultimate leaf segments) 25–30 × 4–7 mm, dimidiate, shortly petiolate, base of acroscopic side of pinnule parallel to costa and base of basiscopic side perpendicular to costa, overall shape being rectangular in the lower half and asymmetrically triangular in the upper, with the apex often sweeping round to the apex of the pinna; apical pinnule asymmetric, trullate-hastate, apex acute; *rachides* reddish black, shiny, densely covered with filiform or arachnoid toothed scales usually one cell wide except at plate-like base, similar scales found on the veins of the pinna segments. *Sori* continuous along margins in upper part of segment; *indusium* narrow continuous, entire; *spores* abortive. Sporophytic chromosome number 2n = 60 (diploid), meiosis mostly irregular.

Type: TRINIDAD, Tacarigua Ward, Tunapuna, 2 miles along Caura Road, *c.* 60 m alt., on shady bank, 3 April 1966, *M. G. & T. G. Walker* T10588 (BM – holotype; herb. Walker – isotype).

Paratypes: TRINIDAD, Tacarigua Ward, same locality and date, *M. G. & T. G. Walker* T10589 (TRIN), T10590 (NY); T10591 (CR), T10592 (BM).

The hybrid and its cytology are discussed by Walker (1985) and illustrated with its parents in figs 12–13 and tables 7 & 8 of that paper. It appears that occasionally a spore mother cell functions and has the potential of producing viable spores.

Adiantum ×*villosolucidum* may be distinguished from *A. lucidum* in having 1–3 pairs of compound pinnae towards the base of the frond and the ultimate segments are shorter, less fleshy, with a polished petiole. From *A. villosum* it differs in having fewer compound pinnae, in the thicker texture, and less crowded ultimate segments. From the *A. latifolium–petiolatum* complex it may be distinguished by its continuous sori.

4. **Sphaerocionium ×tucuchense** Jermy and T. Walker, **hybrida nova**

[? *S. elegans* Sprengel × *S. hirsutum* (L.) C. Presl] (Fig. 5)

Sphaerocionium habitu morphologiaque primo aspectu *S. hirsuto* (L.) C. Presl simillimum, sed manifeste sterile, sporangiis aggregatis indehiscentibus. A *S. hirsuto* stipite tantum in dimidio superiore vel duobus trientibus alato et pilis simplicibus tantum in parte inferiore non alata differt.

Plant forming a dense mat; *rhizomes* slender branched and long-creeping, hairy. *Frond* ± erect, 60–80 mm; *stipe* 15–25 mm, red-brown, with simple hairs, upper half or occasionally two thirds narrowly winged, wing with forked hairs on margin; *lamina* 50–60 × 20 mm, broadly lanceolate, pinnate-pinnatisect; *pinnae* ovate or rounded-trullate, apex rounded, lamina tissue decurrent into rachis, pinnules sometimes forked, ultimate segments linear with rounded apex, margin entire or irregularly and shallowly toothed, with forked crisp pale brown or gingery hairs. *Sori* formed at the apices of ultimate segments in upper part of frond; *indusium* of two ± orbicular lobes; receptacle short but sporangia protruding beyond indusium; *spores* abortive. Chromosome number = 72, meiosis showing unequal pairing.

Type: TRINIDAD, Tacarigua Ward, El Tucuche, 840 m alt., in montane forest, forming large mat on tree trunk, 7 August 1963, *A. C. Jermy & T. G. Walker* J2761 (cytol. ref. no. T6898) (BM – holotype; CR, F, GH, NY, TRIN, U, US, herb. Walker – isotypes).

Paratypes: TRINIDAD, Botanic Gardens Herbarium No. 1203, locality and collector unknown, *c.* 1880 (TRIN). Arima Ward, off Arima–Blanchisseuse road, trackway to Las Lapas, *c.* 550 m, on rotting log on ground at edge of lower montane forest, *T. G. Walker* T6571 (BM, herb. Walker); same locality and population, *A. C. Jermy* 2450 (BM).

Plants very similar in morphology and habit to *Sphaerocionium hirsutum*, but differ in having the stipe winged only in the upper half or two thirds, and simple hairs only on the unwinged lower

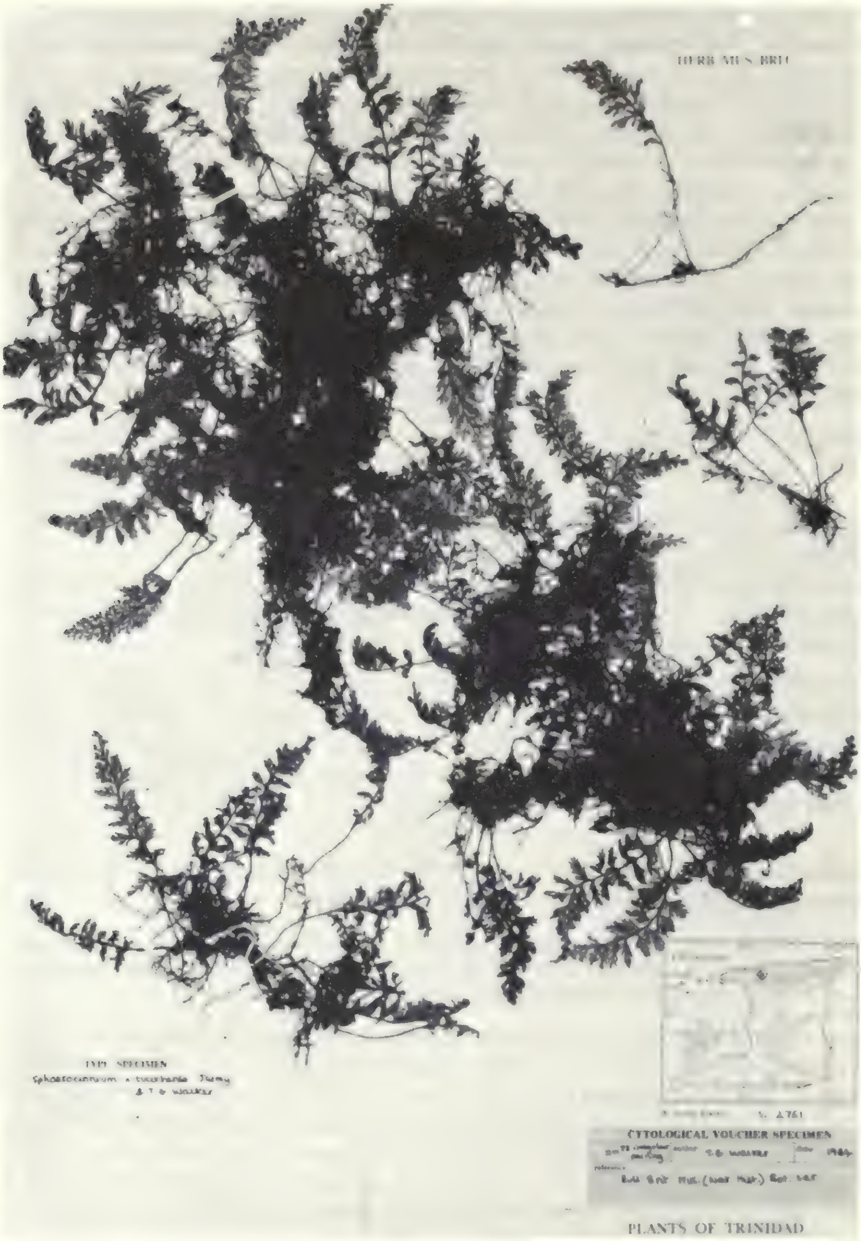


Fig. 5 Holotype specimen of *Sphaerocionium* ×*tucuchense* Jermy & T. Walker (BM).

portion. It is obviously sterile with crowded, undehisced sporangia in each sorus. The morphology of the hybrid and parents are given in Walker (1985: table 10).

5. **Gleichenia interjecta** Jermy and T. Walker, **species nova** (Fig. 6)

Gleichenia interjecta inter *G. bifidam* (Willd.) Sprengel et *G. remotam* (Kaulf.) Sprengel quasi intermedia et ex hybridatione harum specierum verisimiliter exorta. E *G. bifida* cui simillima gemmis apicalibus paleis atro-ferrugineis marginibus latis scariosis fimbriatis vestitis, pilis arachnoideis in superficie laminae abaxiali paucioribus, superficie adaxiali rhachidum ultimarum in maturitate fere glabra, et segmentis laminae in ramo infimo rhachidis seorsum dispositis distinguenda.

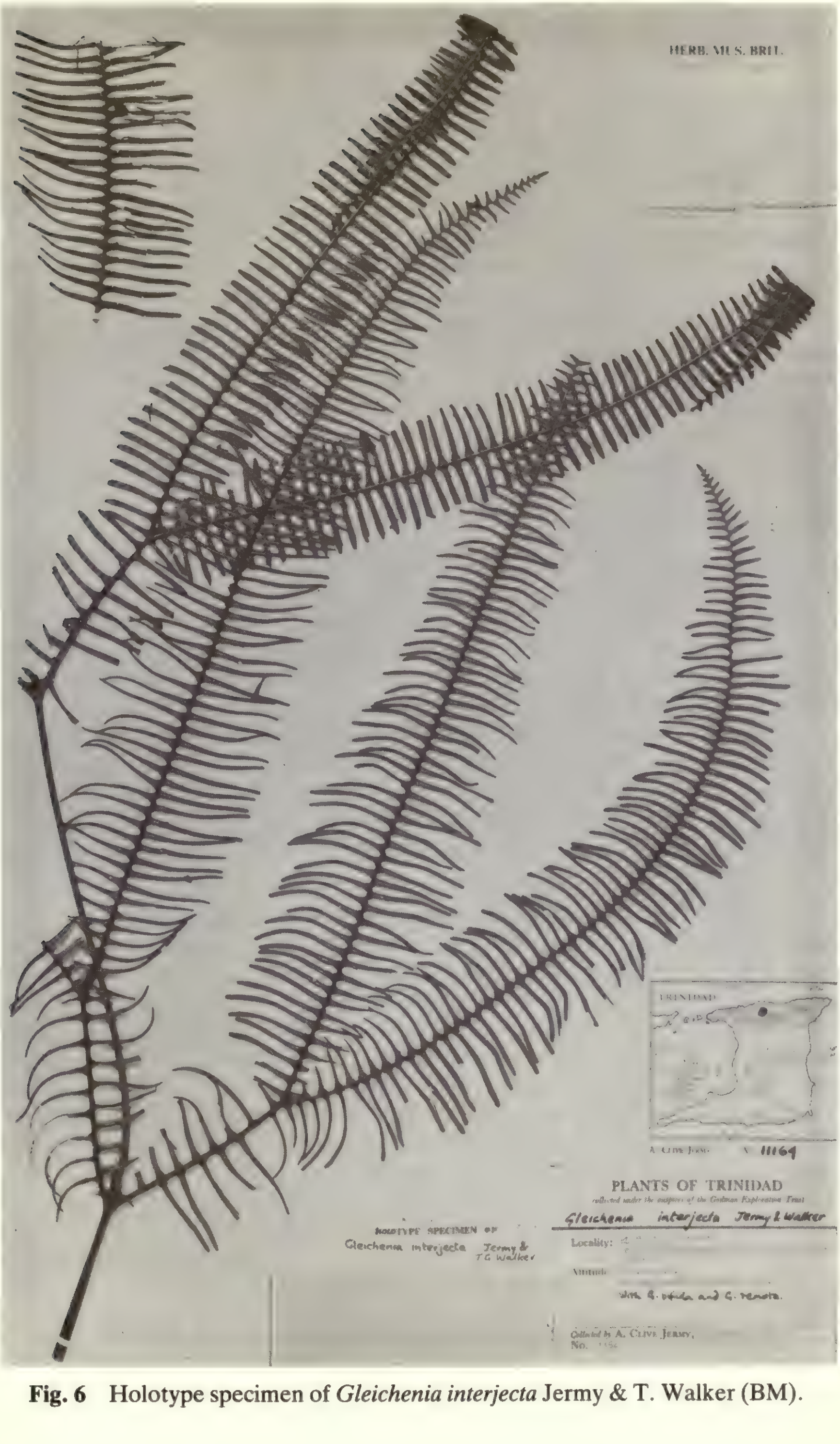

HERB. MUS. BRIT.
TRINIDAD
A. CLIVE JERMY No 11164
PLANTS OF TRINIDAD
collected under the auspices of the Godman Exploration Trust
Gleichenia interjecta Jermy & Walker
Locality:
Altitude
with G. bifida and G. remota.
Collected by A. CLIVE JERMY,
No.
HOLOTYPE SPECIMEN OF
Gleichenia interjecta Jermy & T G Walker

Fig. 6 Holotype specimen of *Gleichenia interjecta* Jermy & T. Walker (BM).

A scrambling robust plant typical of the genus in general habit, often several metres tall. *Rhizome* long-creeping, slender, bearing well-spaced stipes. *Stipes* erect, of varying length, dark cinnamon-brown, more purplish towards base, becoming shiny and naked. *Frond* branch-system arising from apical bud twice-forked; *dormant buds* covered in ovate-triangular, attenuate, dark red-brown scales, 1·5 × 0·4 mm, with broad, scarious, fimbriate margins; *rachides* similar in colour to stipe, initially, with scattered scales as above and puberulent with colourless arachnoid fibrillae, *c.* 0·2 mm long; *primary rachis* exlaminate; 25–30 cm, erect, soon becoming glabrous and shiny; *secondary* and *tertiary rachides* red-brown, bearing frond lamina as pinnately-arranged linear segments, secondary rachis 7–9 cm long, lamina-segments 25–50 (–70) × *c.* 2 mm, *c.* 8 mm apart, interconnected by chartaceous brown rachis-wing, tertiary rachis (ultimate lamina branch) 32–35 cm long, with regularly spaced segments 25–35 × *c.* 2 mm, touching at the base, adjacent segments often markedly uneven in length, gradually becoming shorter in upper third towards apex of the lamina branch, underside of rachis and costae covered with broadly-triangular, attenuate scales as described above and whitish, arachnoid fibrillae arising from a 1- or 2-celled basal plate; lamina tissue mid to dark green above, somewhat glaucous beneath, lower surface densely papillate, with scattered arachnoid fibrillae and similar but unbranched hairs; stomata *c.* 43·5 μm long. *Sori* of 2 or 3, occasionally 4, sporangia; *spores* 45–($\bar{M}$49·5)–52·5 μm, finely punctate-foveolate. Gametophyte chromosome number = 68 (tetraploid), meiosis regular.

Type: TRINIDAD, Blanchisseuse Ward, just south of Blanchisseuse at 20-mile post on road from Arima, 60 m alt., on open bank at forest edge with *G. bifida* and *G. remota*, 9 November 1974, *A. C. Jermy* 11164 (BM – holotype; TRIN – isotype).

Paratypes: TRINIDAD, Blanchisseuse Ward, same locality and date, *A. C. Jermy* 11163 (TRIN), 11170 (NY). Arima Ward, Blanchisseuse Road, 300 m alt., on roadside bank, 19 July 1963, *A. C. Jermy* 2366 (BM, COL, US, VEN); Aripo valley road between 2 and 3 mile posts, 70 m alt., on steep roadside bank, 3 April 1966, *T. G. Walker* T10332 (BM, herb. Walker); La Laja at head of Guanapo valley on S. slope of Morne Bleu, 450 m alt., on roadside bank by cocoa plantation, 1 November 1974, *A. C. Jermy* 11034 (CR, herb. Walker); Aripo Savanna, 30 m alt., covering large areas on open bank at edge of forest, 3 November 1974, *A. C. Jermy* 11105 (BM, U). Tacarigua Ward, Caura Road, *c.* 3 miles up valley, 60 m alt., on steep bank on shale, 6 July 1963, *A. C. Jermy* 2047 (AAU, BM, TRIN).

Gleichenia interjecta, a tetraploid, is intermediate in morphology between the two diploids *G. bifida* (Willd.) Sprengel and *G. remota* (Kaulf.) Sprengel, and most likely formed from hybridization of these species which grow together frequently in Trinidad. This aspect and a comparison of the morphology of the three species has been discussed by Walker (1985: 185–191). *G. interjecta* may best be compared to *G. bifida*, from which it is distinguished by having apical buds covered in darker red-brown scales with broad scarious fimbriate margins, fewer arachnoid hairs on the lower surface of the lamina, in being almost naked on the adaxial side of the mature tertiary (ultimate) rachides (see Walker, 1985: fig. 18C), and in having distinctly spaced lamina segments on the secondary rachides. Furthermore the ultimate lamina branch has the longest leaf segments at the very base. *G. remota*, on the other hand, may be distinguished by the generally remote lamina segments and the virtually glabrous purplish rachides of the ultimate lamina branches.

As the species most resembles *G. bifida* there existed the possibility that that species might have been described from tetraploid material (i.e. *G. interjecta*). The type specimen of *Mertensia bifida* in herb. Willdenow (B) agrees with the diploid in the tapering outline of the ultimate lamina branch and in the dense indumentum on the underside of the lamina segments.

6. **Gleichenia ×pseudobifida** Jermy & T. Walker, **hybrida nova**

[*G. bifida* (Willd.) Sprengel × *G. interjecta* Jermy & T. Walker] (Fig. 7)

Gleichenia valida sed sterilis, *G. bifidam* (Willd.) Sprengel habitu staturaque simulans. Ab hac specie paleis gemmae apicalis angustioribus, paleis arachnoideis in costis laminisque paucioribus, et costa supra fulvo-purpurea distinguitur. A *G. interjecta* Jermy & T. Walker, parente altero, segmentis foliorum angustioribus, costa infra pallidiore, et segmentis paucis (vel etiam nullis) remotis basi pinnarum differt.

A scrambling plant of 4–5 m. *Stipe and lower rachides* pale brown or cinnamon; initially puberulent with narrowly triangular-attenuate, red-brown or pale brown scales with colourless, fimbriate margins, the smaller scales reduced to arachnoid fibrillae adpressed to the rachis

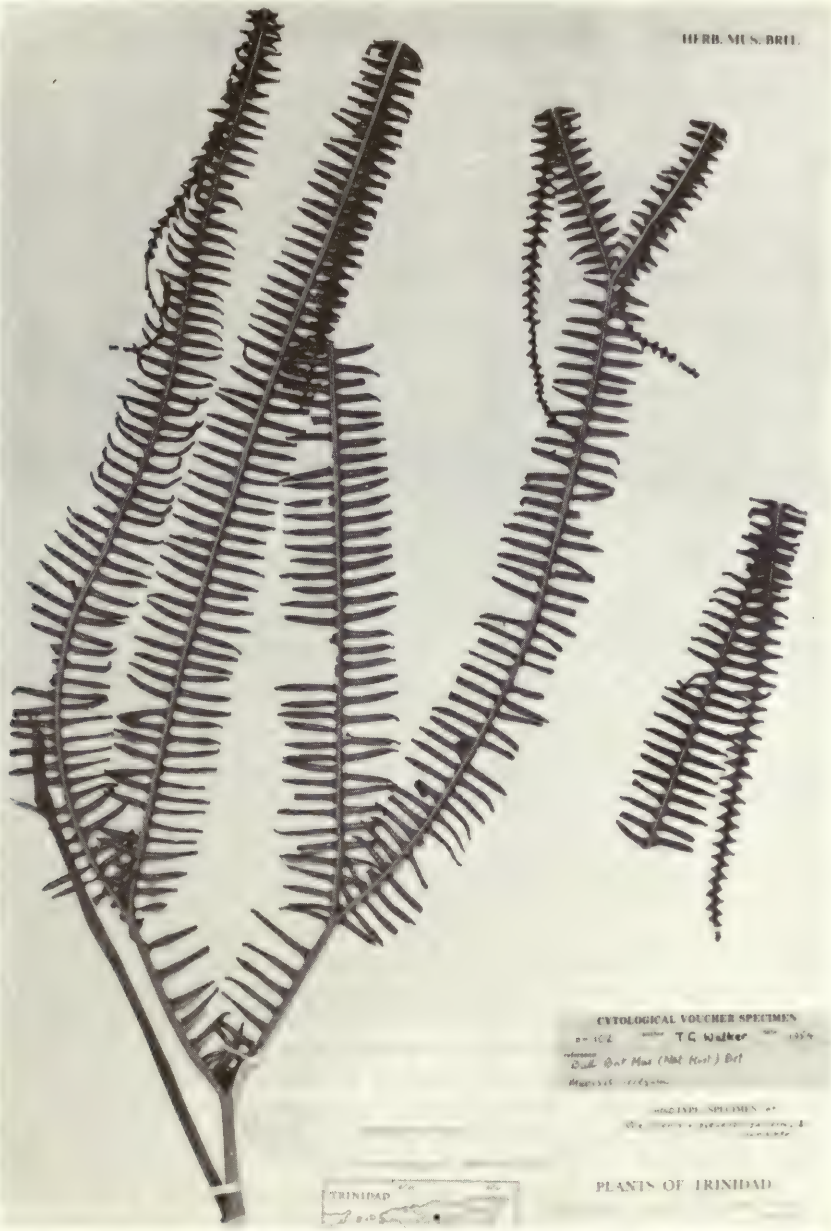


Fig. 7 Holotype specimen of *Gleichenia ×pseudobifida* Jermy & T. Walker (BM).

surface. *Branch system* once or twice forked; dormant buds covered with narrow-triangular mid-brown scales, dilated at base and attenuate at apex, margins paler fimbriate, fibrillae colourless and conspicuous; *primary rachis c.* 7–9 cm long, leaf segments 25–30 (occasionally up to 50) × 3 mm, often on one side only, contiguous except sometimes at very base where 5–8 mm apart; *secondary rachis*, when not the ultimate frond segment, 15–25 cm long, *ultimate frond segment* 25–45 cm long, linear long-attenuate, largest leaf segments 60 × 3 mm, linear, contiguous, costa greenish brown beneath with few prominent, triangular, shortly fimbriate scales, and scattered arachnoid hairs (see Walker, 1985: fig. 18E); mean stomata length 37·5 μm. *Sori* with 2–4 sporangia; spores abortive. Plants triploid with 102 chromosomes, meiosis irregular.

Type: TRINIDAD, Blanchisseuse Ward, Arima–Blanchisseuse Road at 9-mile post, *c.* 450 m alt., on roadside cutting with parent species, 18 July 1963, *T. G. Walker* T6414 (BM – holotype; TRIN – isotype).

Paratypes: TRINIDAD, Blanchisseuse Ward, same locality and date, *T. G. Walker* T6415 (NY), T6417 (herb. Walker); Arima–Blanchisseuse road, near 10¼-mile post, *c.* 500 m alt., on roadside bank, 7 April 1966, *M. G. & T. G. Walker* T10801 (CR), T10805 (F), T10806, T10807, T10808 (herb. Walker), T10810, T10811; 2–3 miles up Aripo Valley, 70 m alt., on steep stony roadside bank in sunlight, 3 April 1966, *T. G. Walker* T10306, T10324, T10326, T10327, T10328, T10329, T10330, T10333; Arima–Blanchisseuse road, *c.* 20-mile post, 600 m alt., on open bank with *G. bifida* and *G. remota* at forest edge, 9 November 1974, *A. C. Jermy* 11166 (BM).

A vigorous growing fern resembling *Gleichenia bifida* in stature and growth habit. Apart from its sterility it is distinguished from that species in having narrower apical bud scales (see Walker, 1985: fig. 17B), fewer arachnoid scales on costae and lamina and a purplish-brown costa above. From *G. interjecta* it can be distinguished by the narrower leaf segments, the paler underside of the costae, and in having only a few (or no) remote segments at base of pinna, usually on one side of the rachis only. The morphology of this compared to the following hybrid is given in Walker (1985: table 13).

7. **Gleichenia ×subremota** Jermy & T. Walker, **hybrida nova**

[*G. interjecta* Jermy & T. Walker × *G. remota* (Kaulf.) Sprengel] (Fig. 8)

Gleichenia valida sed sterilis, *G. remotam* (Kaulf.) Sprengel habitu staturaque simulans. Ab hac specie paleis gemmae apicalis dentibus fimbriatis, paleis similaribus sed minoribus fibrillis incoloribus in costis venisque super laminam extendentibus, segmentis in dimidio superiore rhachidum ultimarum contiguis, haud distantibus ut in *G. remota* distinguenda. A *G. interjecta* Jermy & T. Walker superficie rhachidis adaxiali fulvo-purpurea, segmentis in dimidio inferiore rhachidum ultimarum aliquantum remotis differt.

A vigorous scrambling fern resembling *G. remota* in stature and growth habit. *Rhizome* long-creeping. *Fronds* 4–5 m long; stipe and primary rachides glabrous, purple-brown, initially puberulent with ovate to broadly triangular, pale brown scales *c.* 0·2 mm, with colourless or pale fimbriate margins, or with arachnoid hairs arising from a scale-like basal plate, and with occasional larger (1·5 × 0·4 mm) scales with a dark brown centre and scarious fimbriate margin. *Frond branch-system* once or twice forked; dormant buds covered in triangular, purplish-brown scales with paler, short-fimbriate margins; *primary rachis c.* 8·5 cm long, with linear lamina segments 25 × 2 mm, about 5–8 mm apart connected by a narrow cartilaginous wing, often caducous; paired *secondary rachides* often unequal in length, 14–28 cm long, purplish-brown, *ultimate frond segment* 30–50 cm, ovate-lanceolate in outline, gradually narrowed to tip; *lamina segments* linear, uneven in length, 20–40 × 2–3 mm, their bases touching except for the lowermost segments; underside of rachis with pale triangular scales 1·5 mm long with scarious, fimbriate margins, costae with colourless arachnoid fibrils spreading across papillate lamina surface (see Walker, 1985: fig. 18D); mean stomatal length 37 μm. *Sori* with 2–4 sporangia; spores abortive. Plants triploid with 102 chromosomes, meiosis irregular.

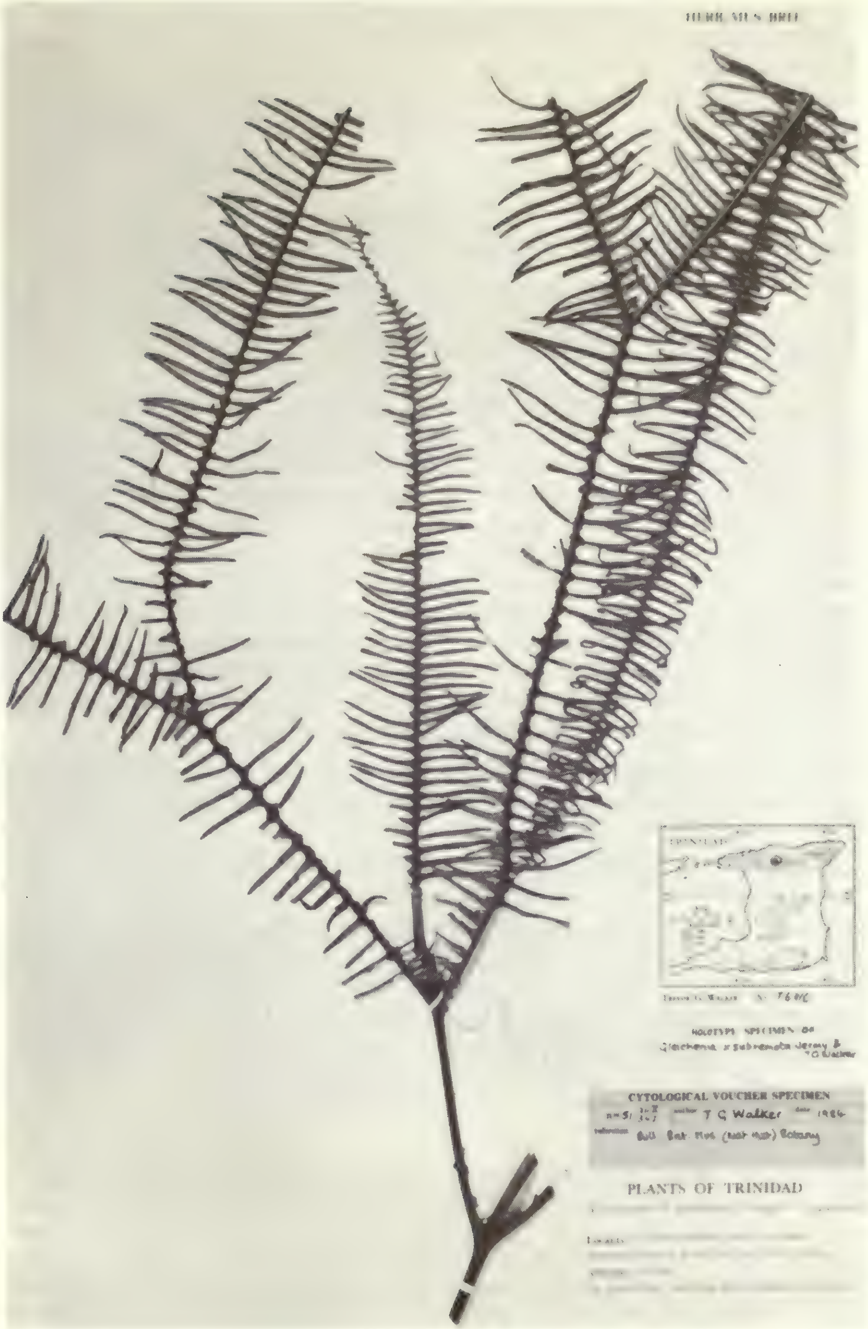

HOLOTYPE SPECIMEN OF
Gleichenia × subremota Jermy & T G Walker
CYTOLOGICAL VOUCHER SPECIMEN
T G Walker
PLANTS OF TRINIDAD

Fig. 8 Holotype specimen of *Gleichenia* ×*subremota* Jermy & T. Walker (BM).

Type: TRINIDAD, Arima Ward, Arima–Blanchisseuse road, *c.* 9-mile post, *c.* 450 m alt., at edge of forest by roadside cutting, 18 July 1963, *T. G. Walker* T6416 (BM – holotype; TRIN, herb. Walker – isotypes).

This vigorous fern usually grows with its parents, *Gleichenia interjecta* and *G. remota*, and is very similar to the latter although its sterility is a useful indicator. From *G. remota* it may be distinguished by having apical bud scales with distinct fimbriate margins (see Walker, 1985: fig. 17E) and similar but smaller scales with colourless fibrillae on the costae and veins, spreading on to the lamina; the ultimate frond branches display contiguous segments in the upper half in contrast to those spaced segments in *G. remota*. From *G. interjecta* it may be distinguished by the purple-brown colour of the upper (adaxial) surface of the rachis, and the lamina segments being somewhat remote in the lower half of the ultimate frond branch.

8. **Goniopteris ×tabaquitensis** Jermy & T. Walker, **hybrida nova**

[*G. paucijuga* (Klotzsch) Pichi-Serm. × *G. tetragona* (Swartz) C. Presl] (Fig. 9)

Planta inter parentes intermedia, a *Goniopteris paucijuga* (Klotzsch) Pichi-Serm. pinnis breviter petiolatis pilis in margine costaque et sparse in pagina adaxiali distincta. A *G. tetragona* (Swartz) C. Presl apice frondis pinnatifido, gemma prolifica vel ad apicem vel in axillis pinnarum superiorum, indusio pubescenti, et sporangiis glabris differt.

Rhizome shortly creeping with 3–5 fronds at apex. *Fronds* variable in size, those produced early in the year sterile and usually smaller than the fertile later ones which often reach 65 cm long, young fronds pinkish with few colourless, ovate, clathrate scales; *stipe* 33–37 cm (those of sterile fronds 7–10 cm) evenly stramineous, scantily furfuraceous in adaxial groove; *lamina* 25–30 cm (sterile > 15 cm) lanceolate-narrowly triangular, pinnate becoming pinnatisect-pinnatifid at apex; *lowermost pinnae* sessile, inflexed, 90 × 23 mm, lanceolate, attenuate at apex, pinnatifid, other pinnae sessile, with occasional adventitious buds in axils of upper pairs, 80 × 18 mm decreasing upwards, linear-lanceolate, apex attenuate, pinnatifid, margins entire with short stiff hairs; *rachis, costae* and *costules* stramineous with sparse short crisp hairs which are also seen on the lamina and veins of the abaxial side, first and second pairs of veins joining below or at the sinus. *Sori* nearer margin than costa; *indusium* with few long hairs; *sporangia* glabrous; *spores* abortive. Chromosome number n = 108 (triploid), meiosis irregular.

Type: TRINIDAD, Charuma Ward, Central Ranges, near Forest Resthouse at Tabaquite, 4 miles N. of Brickfield, *c.* 45 m alt., in partially disturbed seasonal forest, 9 July 1963, *T. G. Walker* T6192 (BM – holotype).

Paratypes: TRINIDAD, Charuma Ward, same locality and date, *A. C. Jermy* 2167 (UC); 2168 (TRIN); *T. G. Walker* T6191, T6193–6 (herb. Walker).

A plant intermediate between the parents, differing from *Goniopteris paucijuga* in having shortly stalked pinnae with hairs on the margins and in being more hairy on costae, costules, and veins. From *G. tetragona* it differs in having a pinnatifid frond apex with a proliferous bud there or in the axils of the upper pinnae, a hairy indusium, and glabrous sporangia. The cytology and comparative morphology are discussed by Walker (1985: figs 34C & D and table 15).

9. **Diplazium ×papyraceum** Jermy & T. Walker, **hybrida nova**

(Fig. 10)

Rhizoma breviter repens, paleis paucis anguste triangularibus clathratis purpurascentibus obsitum. *Frondes* 30–50 cm, ± erectae paucae; stipes 15–22 cm, paulo brevior lamina griseo-virescens alis angustis atris, mox glabrescens; *lamina* 25–30 × 12–17 cm, ovato-triangularis, pinnata pinna terminali; *pinnae* 70–85 × 15–22 mm, breviter petiolatae; *pinnae inferiores* lineari-lanceolatae basi inaequales, latere acroscopico quadrato truncato, basiscopico acute cuneato, apicibus acutis vel attenuatis, marginibus grosse serratis; *pinnae superiores* basi quasi aequales utrinque cuneatae, apicibus plus attenuatis; *pinna terminalis* 70–90 mm, trullata vel hastata, infra margine profunde rotundeque lobato supra grosse serrato, apice acuto; *rhachis* stipiti similis paleis angustissimis triangularibus clathratis dentatis dispersis; costae paleis similibus vel filiformibus paucis et pilis ? glandulosis; venae pilis 2–3-cellularibus, glandulosis. *Sori* secus venam lineari-arcuati indusio angusto integro vel margine subtiliter fimbriato; *sporae* abortivae.

Rhizome very shortly creeping with few clathrate purplish narrowly triangular scales. *Fronds* 30–50 cm, ± erect, few; *stipe* 15–22 cm, slightly less than the blade length, grey-green with narrow black wings, soon glabrous; *lamina* 25–30 × 12–17 cm, ovate-triangular, pinnate with terminal pinna; *pinnae* 70–85 × 15–22 mm, shortly petiolate, lower pinnae linear lanceolate with

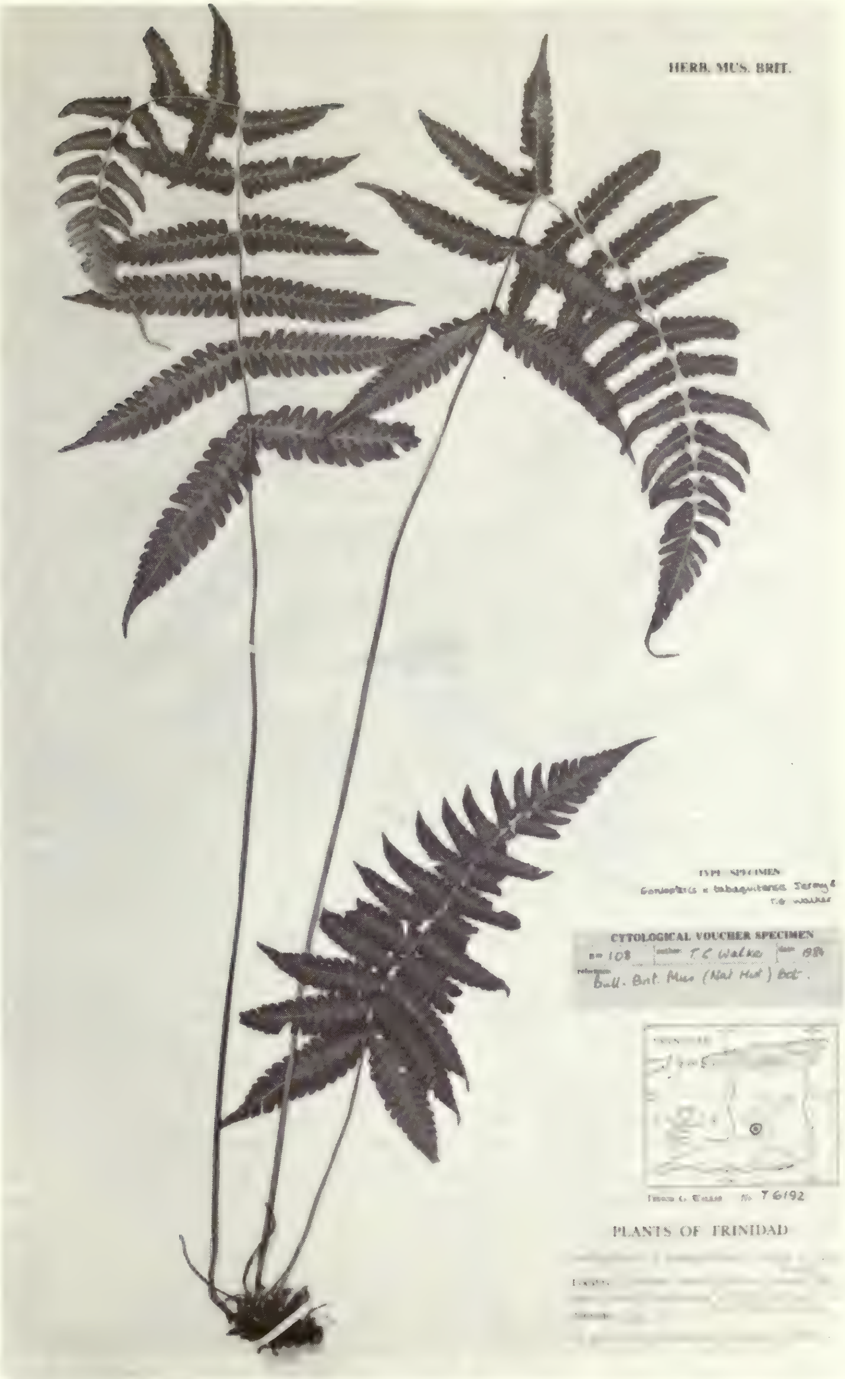

HERB. MUS. BRIT.
TYPE SPECIMEN
CYTOLOGICAL VOUCHER SPECIMEN
n= 108
T.C. Walker
Bull. Brit. Mus. (Nat. Hist.) Bot.
No. T 6192
PLANTS OF TRINIDAD

Fig. 9 Holotype specimen of *Goniopteris* ×*tabaquitensis* Jermy & T. Walker (BM).

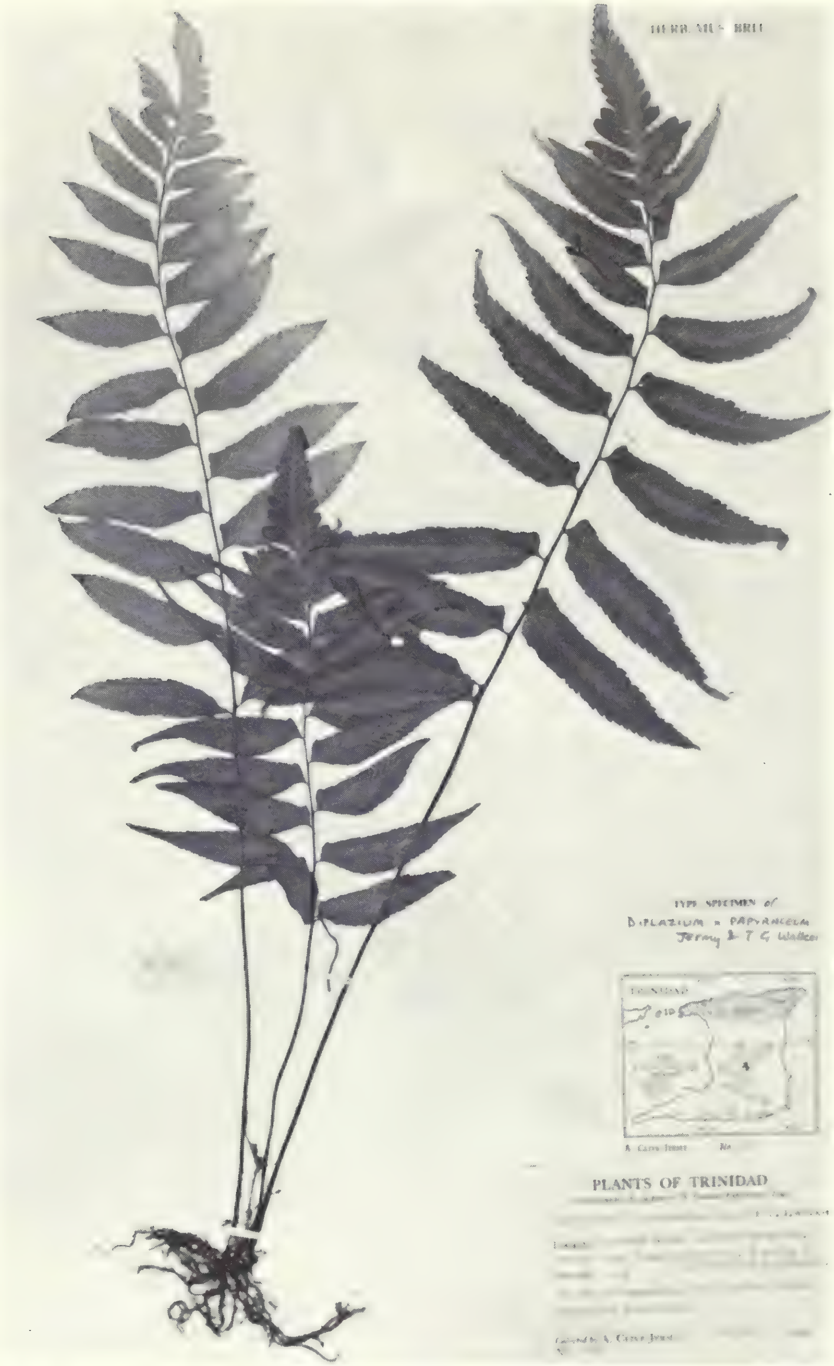

HERB. MUS. BRIT.
TYPE SPECIMEN of
DIPLAZIUM × PAPYRACEUM
Jermy & T G Walker
PLANTS OF TRINIDAD
A. Cave Jermy

Fig. 10 Paratype specimen of *Diplazium* ×*papyraceum* Jermy & T. Walker (BM).

unequal base, that on acroscopic side squarely truncate, on the basiscopic side sharply cuneate, apices acute or attenuate, margins coarsely serrated; upper pinnae with more equal cuneate base and more attenuate apices; *terminal pinna* 70–90 mm long, trullate or hastate, with lower margin deeply and roundly lobed, coarsely serrate above, apex acute; *rachis* as stipe with occasional very narrow, triangular, toothed, clathrate scales, costae with few similar or filiform scales and ?glandular hairs, veins with 2–3-celled glandular hairs. *Sori* linear-arcuate along vein, *indusiate* with narrow entire or finely fimbriate indusium; *spores* abortive. Chromosome number n = 123 (triploid), meiosis irregular.

Type: TRINIDAD, Charuma Ward, Central Range Forest Reserve, Brickfields Teak Plantation, 3 miles S. of Forest Resthouse, 60 m alt., in wet ground by stream, 9 July 1963, *T. G. Walker* T6179 (BM – holotype).

Paratypes: TRINIDAD, Charuma Ward, same locality, population and date, *T. G. Walker* T6176 (TRIN), T6180 (herb. Walker); same locality and date, in aroid communities on floor of mixed forest in high shade, *A. C. Jermy* 2178 (BM).

This specimen had all the appearance of an *Asplenium*, and its cytology alone gave the authors confidence in placing it in *Diplazium*. It is even more curious as, at the time of collection, no obvious close taxa were seen that could be putative parents. It has some similarities to *D. trinitense* Maxon (an endemic of the Northern Range) in rhizome, scales, stipe, rachis morphology, and in the simple pinnate frond, and that species may be one parent.

10. **Ctenitis kallooi** Jermy & T. Walker, **species nova**

(Fig. 11)

Rhizoma erectum, apice paleis triangulo-attenuatis usque ad 13 mm longis 0·5 mm latis, clathratis nitentibus spadiceo-purpurascentibus marginibus dentatis vestito. *Frondes* 50–56 cm; *stipes c.* 20 cm, vivus ferrugineo-purpurascens teresque murinus et sulcatus in sicco, paleis eis rhizomatis similibus et pilis brevibus in superficie adaxiali; *lamina* 37–41 × 23–28 cm, ovata basi bipinnata-pinnatisecta supra minus dissecta, apice ± attenuata; *pinnae infimae* asymmetrico-triangulares pinnula basiscopica infima fere 2-plo acroscopica longiore; *pinnae mediae superaeque* lineari-lanceolatae apice acuto parum acuminato, segmentis ultimis linearibus apicibus truncatis vel rotundatis; *rhachis* supra griseo-virescens infra purpurascens, paleis angusto-triangularibus atro-violaceis et in superficie adaxiali pilis brevibus crispatis; costae paleis similaribus utrinque sparsis, in abaxiali pilis acicularibus 5-cellulis longis; costulae pilis similaribus utrinque; laminae textura tenuis hebes secus venas at super laminam sparse pubescens, margine integro pilis brevibus, stomatibus 37·0–(M̄42·5)–48·0 μm longis. *Sori* in vena acroscopica costulae proxima, exindusiati, paraphysibus absentibus; sporangia cellulis annularibus 13–14; *sporae* 37·5–(M̄40·5)–44·5 μm, cristatae cristis angustis serratis.

Rhizome erect, apex covered with shiny purplish brown, triangular-attenuate, clathrate scales, up to 13 mm long, 0·5 mm wide, with toothed margins. *Fronds* 50–56 cm; *stipe c.* 20 cm long, purple-brown and terete when fresh becoming grey-brown and grooved on drying, with similar scales to those on rhizome and short hairs on the adaxial surface; *lamina* 37–41 × 23–28 cm, ovate, apex ± attenuate, bipinnate-pinnatisect below, less compound above; *lowermost pinnae* asymmetric-triangular with lowest basiscopic pinnule almost twice as long as acroscopic; *middle and upper pinnae* linear-lanceolate, with acute or slightly tapered apex, ultimate segments linear with truncate or rounded apices; *rachis* greenish-grey above, purplish below, with narrow-triangular, purplish-black scales and short crisp hairs on adaxial side; *costae* with similar scattered scales beneath and with 5-celled acicular hairs on both surfaces, similar hairs on both underside and upperside of costules; laminar tissue thin, dull, sparsely hairy along veins and on blade above, margin entire, with short hairs; stoma length 37·0–(M̄42·5)–48·0 μm. *Sori* on acroscopic vein closest to costule, exindusiate lacking paraphyses; *sporangia* with 13–14 annular cells; *spores* 37·5–(M̄40·5)–44·5 μm, cristate, with narrow serrated ridges. Gametophytic chromosome number n = 41 (diploid).

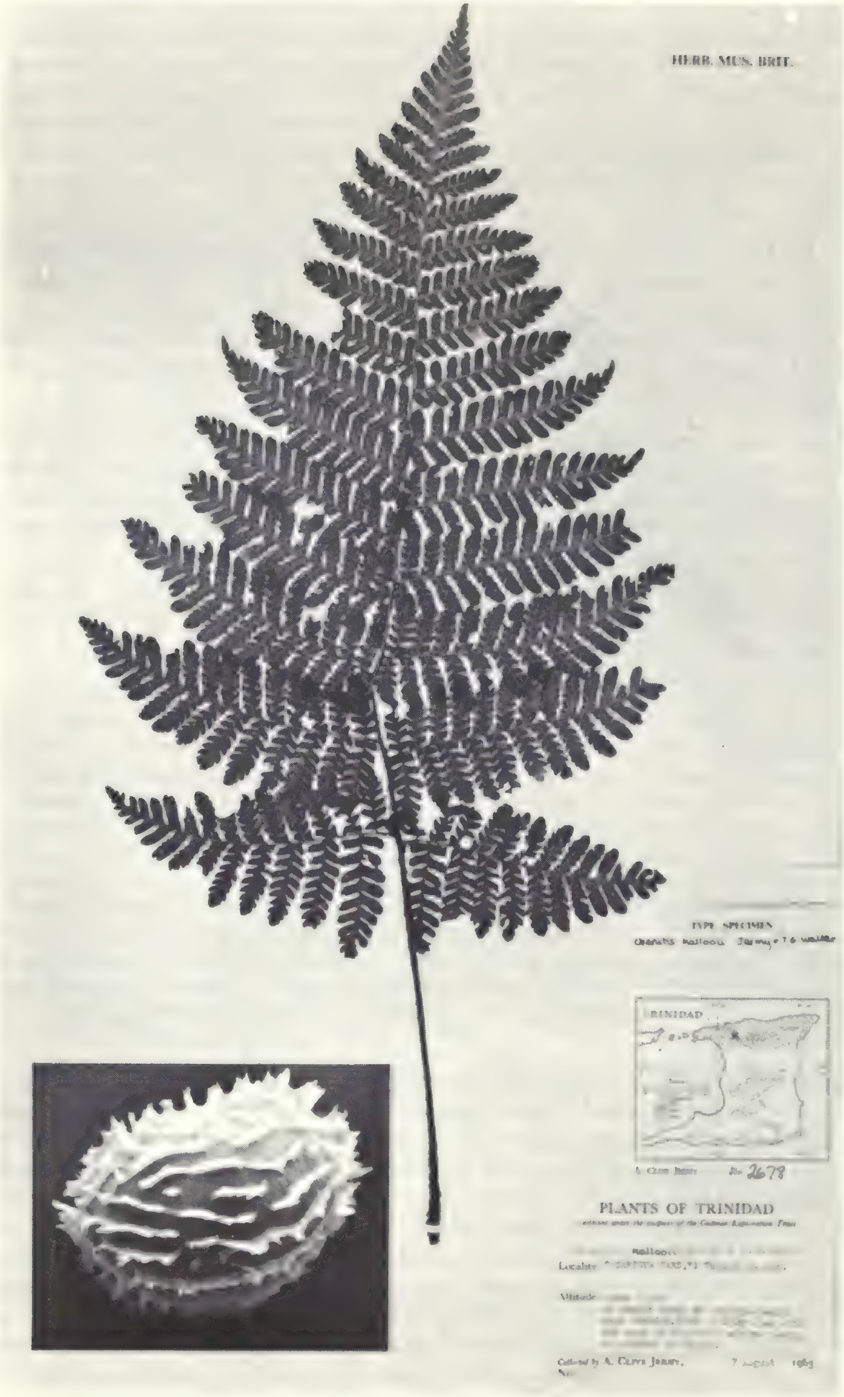

HERB. MUS. BRIT.
TYPE SPECIMEN
Ctenitis kallooi Jermy & T.G. Walker
TRINIDAD
No 2679
PLANTS OF TRINIDAD
kallooi
Locality
Altitude
Collected by A. Clive Jermy, 7 August 1963
No.

Fig. 11 Holotype specimen of *Ctenitis kallooi* Jermy & T. Walker (BM).

Type: TRINIDAD, Tacarigua Ward, El Tucuche massif, *c.* 750 alt., on grassy bank of path through montane forest, 7 August 1963, *A. C. Jermy & T. G. Walker* J2678 (cytol. ref. no. T6793) (BM – holotype; TRIN, herb. Walker – isotypes).

Paratype: TRINIDAD, Tacarigua Ward, same locality and date, *T. G. Walker* T6794 (herb. Walker).

Named after Bhorai Kalloo, Curator at the National Herbarium of Trinidad and Tobago, whose assistance in both the field and herbarium was greatly appreciated.

11. **Tectaria × bulbifera** Jermy & T. Walker, **hybrida nova**

[*T. incisa* Cav. × *T. vivipara* Jermy & T. Walker] (Fig. 12)

Hybrida sterilis ex affinitate specierum *Tectariae incisae* Cav. affinum, *T. viviparae* Jermy & T. Walker similis. Ab hac specie statura parum parviore, pinnis angustioribus, gemmis in axillis pinnarum saepe abortivis, costis costulisque in pagina abaxiali ± glabris et indusio glabro differt.

Plant with erect rhizome. *Fronds* up to 80 cm, ± erect; *stipe* almost as long as the lamina, stramineous to yellow-brown, sparsely scaly at base with sparse glandular hairs on adaxial side, scales 3–6 × 1·5–3·0 mm, ovate-triangular; *lamina* up to 55 × 33 cm, mid to pale green, paper-like when dry, broadly ovate, pinnate, with often abortive buds in pinnae axils; *pinnae c.* 6 pairs, lowermost 12·0–25·5 × 3·5–4·5 cm, shortly petiolate, with a basiscopic lobe ⅓–½ of pinna length, otherwise linear-lanceolate, margin undulate becoming more coarsely lobed towards the attenuate apex; *middle and upper pinnae* only slightly narrower decreasing to 11·5–17·5 cm in length, ± sessile linear-lanceolate, rounded at the base, uppermost decurrent, margins as in lower pinnae; *terminal pinna* 22 cm long, broadly lanceolate with 2–3 deep lobes towards decurrent base; *rachis* similar to stipe in colour and indumentum, 2–3-celled glandular hairs abundant on abaxial side and in axils of pinnae and costae, with similar hairs on adaxial side of costae but ± glabrous beneath, venation areolate with occasional included veins. *Sori* irregularly scattered over leaf surface but where denser, then more regularly on either side of secondary costule; *indusium* peltate, glabrous; *spores* abortive. Chromosome number n = 120 (triploid), meiosis irregular.

Type: TRINIDAD, Charuma Ward, Central Range Forest Reserve, 3 miles S. of Forest Resthouse, Tabaquite, 4 miles N. of Brickfields, *c.* 45 m. alt., 3 July 1963, *T. G. Walker* 6175A (BM – holotype; herb. Walker – isotype).

Paratypes: TRINIDAD, Charuma Ward, same locality and date, on clay bank of rivulet in seasonal forest, *A. C. Jermy* 2147 (BM, TRIN).

This hybrid has been mistaken for *Tectaria vivipara* (*v.i.*) hitherto, and is indeed like a more robust form of that species, with somewhat wider pinnae. The axillary buds are often very small and abortive, the costae and costules are more or less glabrous on the (under) abaxial side, and the indusium is also glabrous in contrast to the hairy one of *T. vivipara*. The abortive sporangia are, of course, diagnostic.

12. **Tectaria orbicularis** Jermy & T. Walker, **species nova**

(Fig. 13)

Rhizoma breviter repens, ascendens. *Frondes c.* 50 cm longae, ± erectae; *stipes* laminam longitudine aequans pallide aurantiaco-ferrugineus, basi fuscatus et leniter gibbus, paleis ovato-triangularibus, 2–4 × 0·75 mm sed plerumque glaber pilis brevibus ? glandulosis in sulco abaxiali ad laminam densioribus; *lamina* 25–32 × 21–25 cm, prasina tenuis glabra late ovata vel orbicularis, trifoliata vel pinnis duabus inferioribus; *pinnae infimae* 15–17 × 3·0–4·5 cm, lineari-lanceolatae, lobo basiscopico unico pinna ⅓ breviore, margine integro grosse undulato; *pinnae mediae* lineari-lanceolatae, sessiles vel adnatae; *pinna terminalis c.* 25 cm longa, basi duobus lobis binatis pinnatisectis aliter lanceolata ad apicem attenuata leniter et irregulariter lobata; *rhachis* stipiti similis; costae prominentes breviter pubescentes supra, infra glabrae, costulis prominentibus in superficiebus ambabus pubescentibus vel glandulosis, infra haud dense; nervatura areolata venulis inclusis. *Sori* in areolis ad costam costulasque proximis irregulares; *indusium* peltatum glabrum; *sporae* 62–69 μm, alis angustis rugosae peridermate verrucoso.

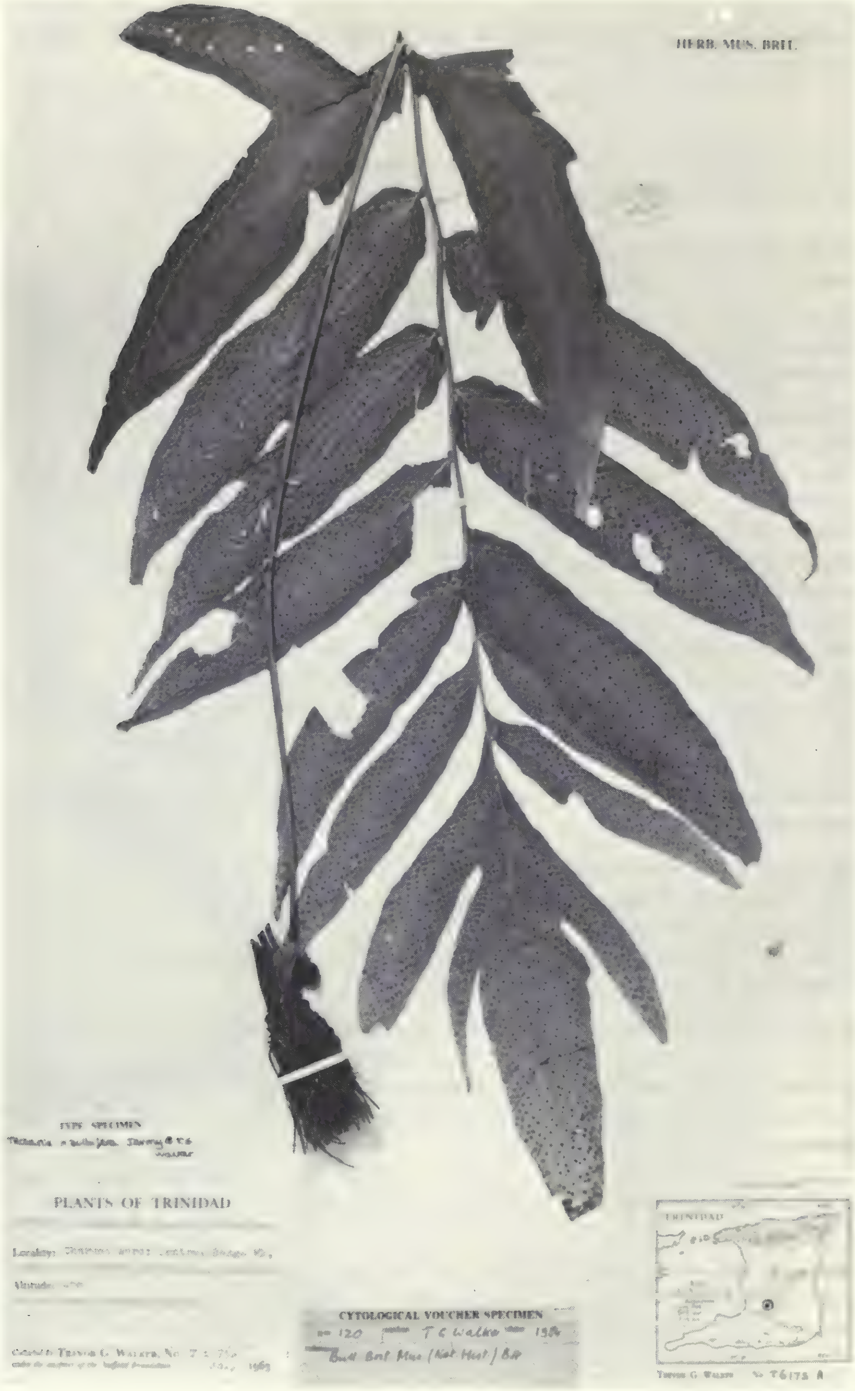

HERB. MUS. BRIT.
TYPE SPECIMEN
PLANTS OF TRINIDAD
Locality:
CYTOLOGICAL VOUCHER SPECIMEN
120
T G Walker
Bull Brit Mus (Nat Hist) Bot
TRINIDAD
T6175 A

Fig. 12 Holotype specimen of *Tectaria* ×*bulbifera* Jermy & T. Walker (BM).

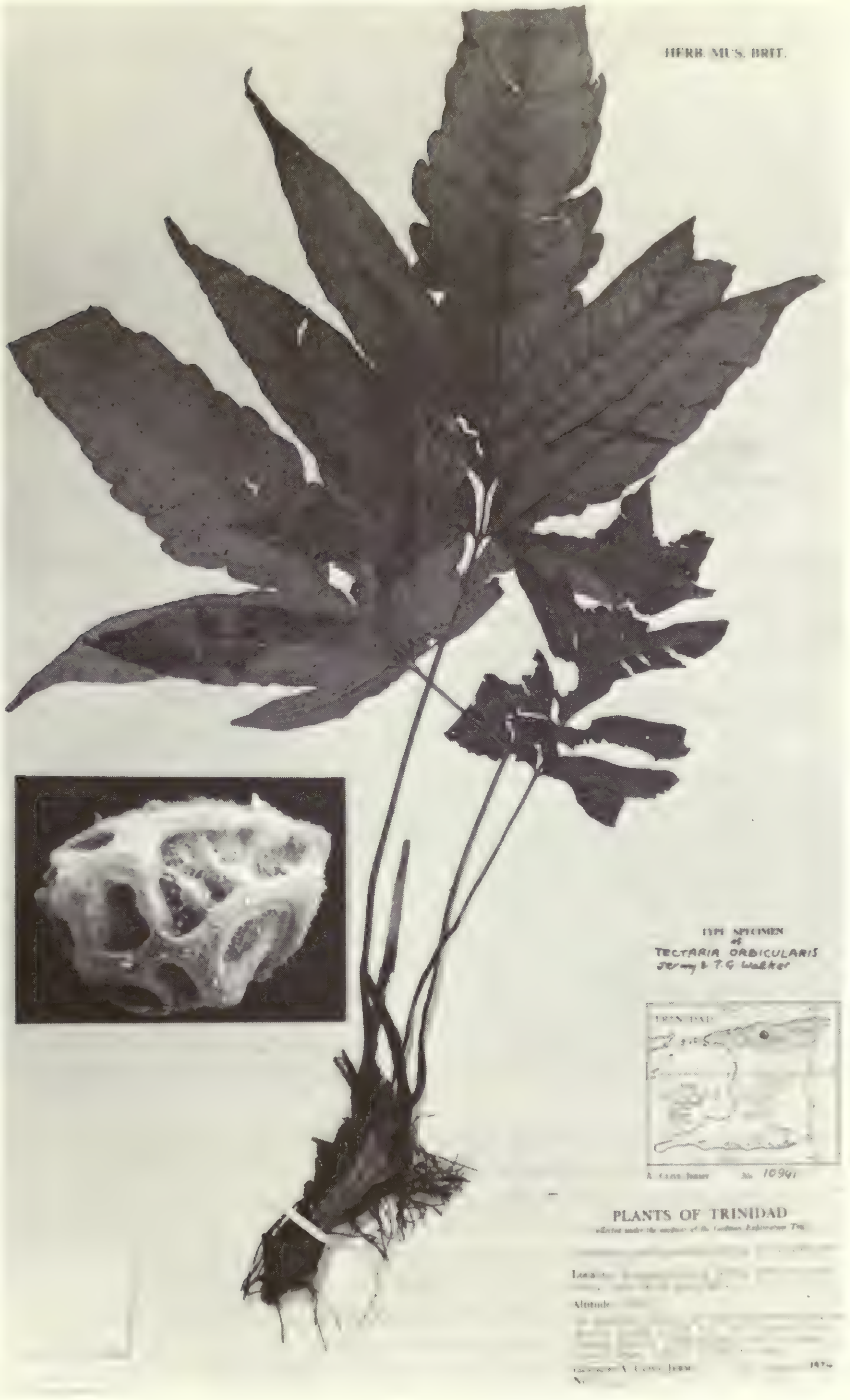

HERB. MUS. BRIT.
TYPE SPECIMEN
of
TECTARIA ORBICULARIS
Jermy & T.G. Walker
TRINIDAD
No. 10941
PLANTS OF TRINIDAD
Altitude

Fig. 13 Holotype specimen of *Tectaria orbicularis* Jermy & T. Walker (BM).

Rhizome shortly creeping, ascending. *Fronds c.* 50 cm long, ± erect; *stipe* as long as lamina, pale orange-brown, base darker, slightly swollen, with few ovate triangular scales, 2–4 × 0·75 mm, otherwise glabrous but with short ? glandular hairs in abaxial groove increasing in density towards lamina; *lamina* 25–32 × 21–25 cm, mid-pale green, tissue thin, glabrous, broadly ovate to orbicular in outline, trifoliate or with two pinnae below; *lowermost pinnae* 15–17 × 3·0–4·5 cm, linear-lanceolate with single basiscopic lobe ⅓ length of pinna, margin entire, coarsely undulating; *middle pinnae* linear-lanceolate, sessile or adnate; *terminal pinna c.* 25 cm long, with 1 pair of pinnatisect lobes at base, otherwise lanceolate attenuate at apex, shallowly and irregularly lobed; *rachis* as stipe; costae prominent, shortly pubescent on the upper side, glabrous on the lower side, costules prominent, pubescent-glandular on both sides but less dense below, venation areolate with included veinlets. *Sori* produced irregularly on areola nearest to costa or costule; *indusium* peltate, glabrous; *spores* 62–69 *μ*m, narrowly winged, rugose, periderm verrucose.

Type: TRINIDAD, Blanchisseuse Ward, Brasso Seco Road just W. of village, 200 m alt., on gentle slope by roadside, area collecting storm water from plantation, 23 October 1974, *A. C. Jermy* 10941 (BM – holotype).

Paratype: TRINIDAD, Blanchisseuse Ward, same locality and date, sent to Royal Botanic Gardens, Kew, as a sporeling *Jermy* 10941: 1 (TRIN).

The paratype specimen was found to be diploid with n = 40 chromosomes, and in this respect it contrasts with *Tectaria incisa* Cav. which is tetraploid. In many respects it is similar to that species and has been included in it in the past. The frond outline is distinctive, *T. incisa* having 3 or 4 pairs of pinnae and therefore more elongate-ovate.

13. **Tectaria ramkissoonii** Jermy & T. Walker, **species nova**
(Fig. 14)

Rhizoma erectum. *Frondes* maximae 120 cm longae, ± erectae vel leviter arcuatae, juvenes roseae paleis hyalinis et stomatophoris conspicuis basin versus stipitis; *stipes* fronde dimidio brevior aurantiaco-ferrugineus, basi paleis paucis ovatis fuscis integris, pilis brevibus glandulosis dense vestitus; *lamina* 45–65 × 25–50 cm, in superficiebus ambabus glanduloso-pubescens aeruginosa anguste ovata vel late lanceolata pinnata; *pinnae* 4–7, sessiles vel breviter petiolatae pinnatisecto-pinnatifidae; *pinnae infimae c.* 24 × 15 cm, segmento basiscopico ad costam secto, quam pinna 3-plo breviore; *pinnae mediae superaeque* lineari-lanceolatae ad apicem attenuatae, lacerae, ad apicem frondis minus; *pinna terminalis* 22 × 11 cm, rhombea basi lacerata lobis infimis et apice attenuatis; *rhachis* spadicea; costa costulaeque similares prominentes pilis glandulosis densis in superficiebus ambabus; nervatura areolata, venulis aliquando inclusis. *Sori* in vena primaria e costula divergente, praeter segmenta grandia basalia irregulariter biseriales; *indusium* peltatum; *sporangia* juvenia rosea, cellulis annularibus 14–16; paraphyses in receptaculo vel seta sporangifera exorientes, plerumque ad apicem cellulis glandulosis geminatis; *sporae* 37·5–($\overline{\mathrm{M}}$52·5)–64·0 *μ*m, alis latis spinulosis.

Rhizome erect. *Fronds* up to 120 cm long, ± erect or gently arching, young fronds pink-red, with colourless scales and conspicuous stomatophores at swollen stipe base; *stipe* half the length of frond, rich orange-brown with few ovate, brown, entire scales at base, densely covered with short glandular hairs; *lamina* 45–65 × 25–50 cm, deep green, glandular pubescent on both surfaces, narrowly ovate to broadly lanceolate, pinnate; *pinnae* 4–7, sessile or shortly petiolate, pinnatisect-pinnatifid; *lowest pinnae c.* 24 × 15 cm with a basiscopic segment cut to costa and ⅓ length of pinna; *middle and upper pinnae* linear lanceolate with an attenuate apex, lacerate, becoming less cut towards apex of frond; *terminal pinna* 22 × 11 cm, rhomboid in outline, lacerate at its base, lowermost lobes and apex attenuate; *rachis* mid-brown, costae and costules similar and prominent, densely glandular hairy on both sides; venation areolate, sometimes with included veinlets. *Sori* arising on a primary vein from the costule and irregularly biseriate except in the larger basal segments; *indusium* peltate; *sporangia* bright pink when young, with 14–16 annular cells, paraphyses arising on receptacle or on sporangial stalk bearing usually pairs of glandular cells at apex; *spores* 37·5–($\overline{\mathrm{M}}$52·5)–64·0 *μ*m, with broad wing, finely echinate. Chromosome number n = 80 (tetraploid).

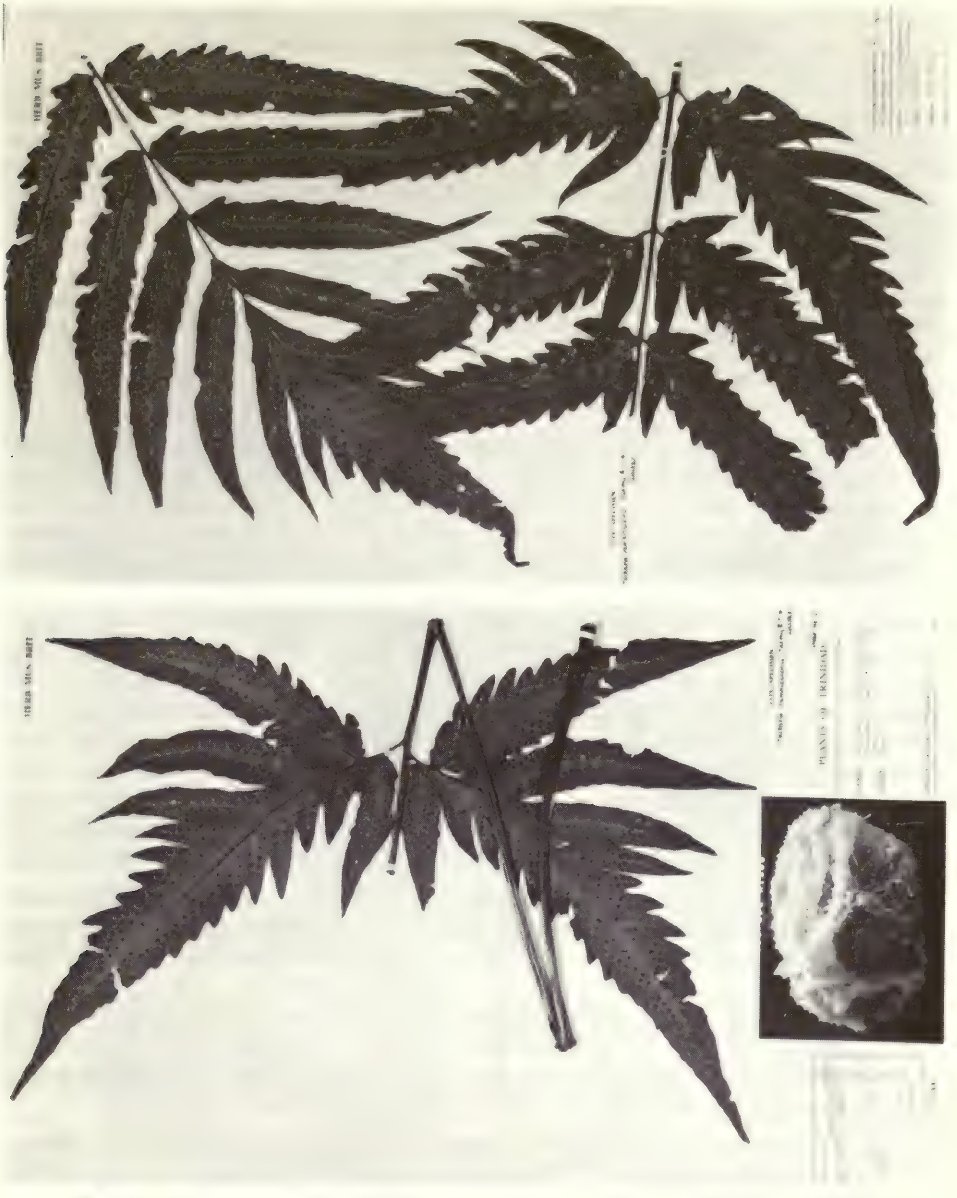


Fig. 14 Holotype specimen of *Tectaria ramkissoonii* Jermy & T. Walker (BM).

Type: TRINIDAD, Arima Ward, Aripo Heights, along path to caves, in montane forest over limestone, *c.* 600 m alt., 26 August 1963, *T. G. Walker* T7088 (BM – holotype; TRIN, herb. Walker – isotypes).

Paratypes: TRINIDAD, Arima Ward, same locality, population, and date, *A. C. Jermy* 3002 (BM, NY, CR, TRIN).

Named after Roodal Ramkissoon, of the University of the West Indies, St Augustine, whose invaluable help in the field was greatly appreciated by the authors.

Hitherto this species would have been included under *Tectaria incisa* Cav. (*T. martinensis* auct.). It differs in the more numerous, narrower pinnae, and the dense indumentum of the lamina, costules, and costae.

14. **Tectaria vivipara** Jermy & T. Walker, **species nova**

[*Tectaria martinicense* (Spreng.) Copel. var. *vivipara* auctores pl.] (Fig. 15)

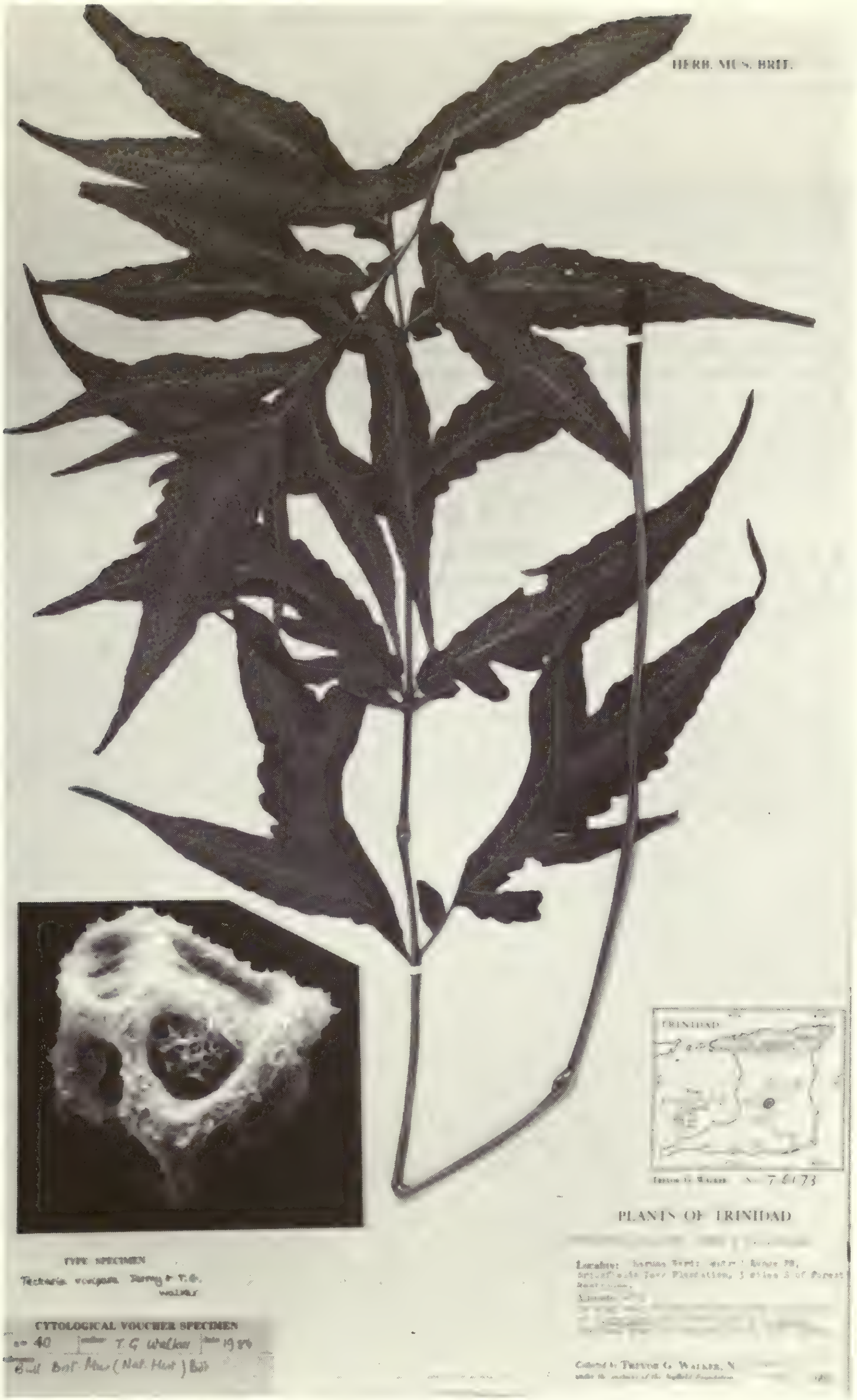
Planta statura habituque *Tectariae incisae* Cav. similis. *Rhizoma* erectum. *Frondes* ± erectae usque ad 105 cm longae in cultura, sylvestres *c.* 60 cm; *stipes* 2–3-plo fronde brevior stramineo-flavescens vel brunneo-rufus, basi paleis sparsis, pilis paucis in sulco adaxiali dispersis, meristemate paleis 3–4 × *c.* 1 mm, ± triangularibus apice longe attenuato, integris tecto; *lamina* 60 × 32 (in cultis) – 40 × 25 cm, prasina late lanceolata pinnata, ad axillas pinnarum vivipara; *pinnae* paribus 6–8, pinna basali 13–21 × 2–3 cm, petiolata lanceolata lobo basiscopico prominenti, acroscopico brevi sed conspicuo, margine irregulariter inciso vel undulato; *pinnae superae* 16–14 × 2·5–2·2 cm, ellipticae vel lanceolatae apice attenuato basi late cuneata vel decurrenti, margine leniter lobato vel sinuato (in holotypo) aut minus lobato (in paratypis); *pinna terminalis* late lanceolata ± profunde lobata, lobis inferioribus in pinnas transientibus; *rhachis* colore stipiti similis sed densius in sulco adaxiali glanduloso-pubescens; costae in superficie adaxiali pubescentia similari in abaxiali minus densa; nervatura areolata, venulis aliquando inclusis. *Sori* uniseriales secus costulam, saepe irregulatim formati; *indusium* peltatum pilis brevibus glandulosis in pagina superiore; *sporae* 43–49 μm, cristatae, sparse papillatae.

Plant similar in stature and habit to *T. incisa* Cav.; rhizome erect. *Fronds* ± erect, up to 105 cm long in cultivated material, in the wild *c.* 60 cm; *stipe* ⅓–½ as long as frond, stramineous or yellowish to deep red-brown, very sparsely scaly at base and a few scattered hairs in adaxial groove, growing point covered in scales 3–4 × *c.* 1 mm ± triangular with long attenuate apex, entire; *lamina* 60 × 32 (in cultivated plants) – 40 × 25 cm, mid-green, broadly lanceolate, pinnate, viviparous at the pinnae axils; *pinnae* 6–8 pairs, basal pinna 13–21 × 2–3 cm, petiolate, with a pronounced basiscopic lobe and with a small but distinct acroscopic basal lobe, lanceolate, margin irregularly cut to undulate; *upper pinnae* 16–14 × 2·5–2·2 cm elliptic to lanceolate, apex attenuate, broadly cuneate to decurrent at base, margin shallowly lobed to sinuate (in holotype), or less lobed (in paratype material); *terminal pinna* broadly lanceolate, ± deeply lobed, lower lobes grading into pinnae; *rachis* similar in colour to stipe but more glandular-pubescent in adaxial groove, costae with similar covering on adaxial side, less dense on abaxial side; venation areolate with occasional included veinlet. *Sori* uniseriate along costule but frequently irregularly formed; *indusium* peltate with short glandular hairs on upper surface; *spores* 43–49 μm, crested, sparsely finely papillate. Chromosome number n = 40 (diploid).

Type: TRINIDAD, Charuma Ward, Central Range Forest Reserve, Brickfields Teak Plantation, 3 miles S. of Forest Resthouse, *c.* 60 m alt., on clay bank by rivulet with mixed population of viviparous and non-viviparous *T. incisa*, 9 July 1963, *T. G. Walker* T6173 (BM – holotype; herb. Walker – isotype).

Paratypes: TRINIDAD, Charuma Ward, same locality and date, *T. G. Walker* T6171 (BM, TRIN); same locality and date, by stream in cut-over seasonal forest, *A. C. Jermy* 2145 (BM, TRIN), 2146 (NY, CR). Arima Ward, road from San Raphael–Cumuto, in cocoa just before iron bridge, 13 May 1927, *Hombersley* 243 (TRIN).

Well known as a viviparous form of *Tectaria incisa* and its synonyms, and widespread throughout the Caribbean and Central America. *T. incisa* in Trinidad is, however, a tetraploid (Walker, 1985) and *T. vivipara* is based on a diploid of known origin and therefore a new type. It is distinguished from *T. incisa* by its vivipary, and hairs on the abaxial side of the costae.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TRINIDAD
PLANTS OF TRINIDAD
TYPE SPECIMEN
Tectaria vivipara Jermy & T.G. Walker
CYTOLOGICAL VOUCHER SPECIMEN
40
T.G. Walker
Bull. Brit. Mus. (Nat. Hist.) Bot.

Fig. 15 Holotype specimen of *Tectaria vivipara* Jermy & T. Walker (BM).

New combination

Meniscium nesioticum (Maxon & C. Morton) Jermy & T. Walker, **comb. nov.**
Basionym: *Dryopteris nesiotica* Maxon & C. Morton in *Bull. Torrey bot. Club* **65**: 362 (1938).

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Walker, T. G. 1985. Cytotaxonomic studies of the ferns of Trinidad 2. The cytology and taxonomic implications. *Bull. Br. Mus. nat. Hist.* (Bot.) **13**: 149–249.

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Bulletin of the British Museum (Natural History)

Some genera of the Biddulphiaceae (diatoms) with interlocking linking spines

Robert Ross & Patricia A. Sims

Botany series Vol 13 No 3 27 June 1985

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Some genera of the Biddulphiaceae (diatoms) with interlocking linking spines

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Synopsis

The diatoms with interlocking linking spines and also large pseudocelli are described in detail and the new morphological terms 'projection' and 'Crawford step' are proposed. These diatoms comprise five genera: *Briggera*, gen. nov. to which we transfer the species with these characters that were previously placed in *Hemiaulus*, *Dicladiopsis* which normally has heterovalvar frustules with only one valve with linking spines, *Strelnikovia*, gen. nov. typified by *Rutilaria antiqua* Streln., *Keratophora,* and *Thaumatonema*. The new taxa *Briggera morenoensis, B. monoligata, B. vemae, B. robusta, B. bonei, B. paratethyos, B. ornithocephala* subsp. *atlantica, Dicladiopsis alta, D. erecta, Strelnikovia tumida, S. inclinata, S. reniformis,* and *S. incerta* are described and named; three others, one each from *Briggera, Dicladiopsis,* and *Strelnikovia*, are described but not named because we had insufficient material.

All representatives of these genera are marine and fossil. They range in age from the upper Turonian-

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Coniacian (upper Cretaceous) to the early Miocene. There are species of *Biddulphia* which resemble some species of *Briggera* extremely closely except for the lack of linking spines, and others equally close to *Strelnikovia* but differing in the same way. The existence of these species brings into question the division of the Biddulphiaceae into the subfamilies Biddulphoideae and Hemiauloideae on the basis of the occurrence of linking spines in the latter.

Introduction

In 1981 the British Museum (Natural History) received from Mr A. L. Brigger of Yucaipa, California, U.S.A., through Prof. R. W. Holmes of the University of California, Santa Barbara, the diatom specimens that he had selected from the many samples in his possession but had not mounted. Both Mr Brigger's personal collection of mounted slides and the samples from which they came are now deposited in the California Academy of Sciences, San Francisco. Many of the specimens used in the preparation of this paper, including almost all those examined with the scanning electron microscope, were part of this gift. It included specimens from the Campanian (upper Cretaceous) deposits from the eastern slopes of the Ural mountains, U.S.S.R., studied by Strel'nikova (1964, 1965, 1974). Amonst these were examples of *Rutilaria antiqua* Streln., a species that she described from that material, expressing doubts as she did so about its generic assignment as it did not have a periplekton. Our examination of this species not only confirmed the absence of a central periplekton but also showed that at the apices of the valve, on the distal side of the slightly raised elevations, it had pseudocelli, not ocelli as in *Rutilaria* Grev.; furthermore, its frustules were united in inseparable chains by a band of interlocking linking spines around the proximal and lateral edges of its elevations. These linking spines are wider above than they are near their bases. These facts showed that this diatom is not a member of the Eupodiscaceae, the family to which *Rutilaria* belongs, but of the Biddulphiaceae, and that it is closely related to, but not congeneric with, the group of *Hemiaulus* spp. with large pseudocelli previously discussed by one of us (Ross, 1972) and shown later by scanning electron microscopy to have interlocking linking spines (Ross, Sims & Hasle, 1977). Amongst the specimens selected by Mr Brigger we found six other species congeneric with *Rutilaria antiqua*, five of them from the Campanian of the eastern Ural mountains and one from the upper Eocene material from 'Kamichev' (for this locality see p. 280 below). The new genus *Strelnikovia* is established below for these species.

These findings caused us to reconsider the group of *Hemialus* spp. with large pseudocelli and interlocking linking spines. Amongst the specimens selected by Mr Brigger we found representatives of seven undescribed taxa with these characteristics, and also specimens of *H. sibericus* Grunow which seemed to share them, although the linking spines were broken on all that we examined. We found an additional undescribed species in the collections of the British Museum (Natural History) and examination of the type of *H. caverna* Brun showed that it too had these characters. These species differ very considerably from most of the species of *Hemiaulus* Heib. (nom. cons. prop., Ross, in press), including its type, and we have accordingly established for them below the new genus *Briggera*. The features that distinguish this genus from *Hemiaulus* sensu stricto are discussed in the taxonomic section of this paper below (p. 286).

We have also recently been able to make a more thorough examination with the scanning electron microscope of specimens of *Keratophora nitida* Pant., the only species of this genus. This has shown that it too has its sibling valves inseparably united by interlocking spines and also that it possesses large pseudocelli on its elevations. Contrary to previously held views (e.g. Brigger & Hanna, 1965; Ross & Sims, 1980), it is not at all closely related to *Kittonia* Grove & Sturt. Examination with the light microscope also showed that both species of *Thaumatonema* Grev. possess the same characteristics, although we have not had available unmounted specimens of either of these to confirm this by scanning electron microscopy. *Dicladiopsis* De Toni is another genus in which interlocking linking spines and large pseudocelli are found, but in this genus it seems probable that the frustules are always heterovalvar, with linking spines present on only one of the two valves, so that the frustules are united in inseparable pairs. This paper is a monographic revision of these five genera, *Briggera, Dicladiopsis, Strelnikovia, Keratophora,* and *Thaumatonema*, treated in that order.

Sources of specimens and records

In the taxonomic section of this paper we give details of the distribution in time and space of all the species with which we deal. This information is derived primarily from specimens that we examined ourselves, but some of it is taken from published literature. The precision with which the actual locality from which a specimen comes is indicated varies appreciably, and in some cases there is even some doubt about its geological age. In this section of the paper we present the information available about the locality and geological age of all the materials from which the specimens or records come. This information is presented in a geographical sequence, beginning with the U.S.S.R. and then the rest of Europe, followed by North America, the North Atlantic Ocean, the Caribbean, the South Atlantic Ocean, the Indian Ocean, and finally New Zealand.

The species with which we are concerned are all fossil and range in age from the Turonian of the upper Cretaceous to the lower Miocene. Because of the comparative lack of precision in the dating of many of the samples, we have grouped them, as far as age is concerned, in the taxonomic section under the following heads:

Upper Cretaceous — upper Turonian–Coniacian
Upper Cretaceous — Senonian, for a record with no more precise date
Upper Cretaceous — Campanian
Upper Cretaceous — Maastrichtian
Paleocene
Lower Eocene
Middle Eocene
Upper Eocene
Lower Oligocene
[Upper Oligocene], without any record
Lower Miocene

However, we give more detail below where it is available.

U.S.S.R.

Tyumen'sk oblast, western Siberia

Amongst the material that the British Museum (Natural History) received from Mr Brigger were specimens from exposure XI (14) from Til'tim in the basin of the river Synya, and from core 82 from one of the wells drilled near Ust'-Man'ya in the basin of the river Severnaya Sos'va, both in Tyumen'sk oblast. Details of these samples are given by Strel'nikova (1965, 1974). They are both of Campanian (upper Cretaceous) age.

Strel'nikova (1974) gives a reference to a paper by Krotov & Shibkova (1961) that we have not seen and states that it includes a record of one of the species with which we are concerned from the Paleocene of the eastern slope of the Ural mountains. The greater part of the area covered by that phrase is in Tyumen'sk oblast.

Paramonova (1964) described the diatom flora of material from the basin of the River Ob from deposits ranging in age from the lower Eocene to the lower Oligocene. We have not included any records from her paper because of uncertainty about her identifications of species from the group with which we deal. However, amongst the specimens received from Mr Brigger are a number from 'N. Siberia, River Ob, late Eocene'. These we presume to have come from one of the samples studied by Paramonova.

Sverdlovsk oblast

Jousé* (in Proshkina-Lavrenko et al., 1949*b*) records two of the species included here from the Paleocene of Sverdlovsk oblast. However, she later (Jousé, 1955) states of one of these two,

---

* In this paper we have used the form 'Jousé' for the name of this author rather than the standard transliteration 'Xhuze' because she herself always used it when writing in the roman alphabet, as have almost all other authors when referring to her works. In all other cases we have given a transliteration of the cyrillic spelling, but these two forms are so different that use of the unfamiliar one would cause confusion.

Hemiaulus sibericus Grunow (*Briggera siberica* (Grunow) R. Ross & P. A. Sims), that it comes from the lower Eocene of the eastern slopes of the Ural mountains and from material of the same age from western Siberia, suggesting a change of opinion about the age of the specimens that she considered Paleocene in 1949.

Jousé (1955) records another species with which we deal, *Keratophora nitida* Pant. (as *Kittonia granulata* Chenev.), from the upper Eocene of Kamyshlov in Sverdlovsk oblast.

A number of the specimens that are cited under various species are labelled as coming from 'Kamichev'. The first account of diatoms from this material was given by Chenevière (1934). It is one of a number of samples from the U.S.S.R. that came into the hands of diatomists in western Europe in the 1930s, and in more than one instance the name of the locality had been mis-transcribed. 'Kamichev' seems to have been one such mis-transcription. Reinhold (1945) considered that 'Kamichev' was an error for Kamyshin in Volvograd oblast and that the sample was of lower Eocene date. However, one of us (Ross, 1972) has pointed out that its diatom flora has more in common with the upper Eocene flora from Kamyshlov than with the lower Eocene flora from the central Volga basin, and Glezer (in Glezer et al., 1974: 136) came to the same conclusion, apparently independently. There seems little doubt that the material labelled 'Kamichev' is of upper Eocene age, but the locality is still somewhat uncertain. There are a number of settlements called Kamyshev or Kamyshevo in the U.S.S.R., including a Kamyshevo at 56° 32′ N, 61° 21′ E in Sverdlovsk oblast about 100 km SW of Kamyshlov, and the same formation may outcrop there. Kamyshlov, however, is the most probable source of the material labelled 'Kamichev'.

Ulyanovsk oblast

Specimens of species with which we deal in this paper are labelled as coming from: Ananino, Archangelsk, Simbirsk, Smolkovo, and Syzran. In spite of the fact that Syzran is in Kuibyshev oblast, it is probable that all these come from Ulyanovsk oblast. Anan'ino (53° 24′ N, 47° 18′ E) and Smol'kovo (53° 43′ N, 47° 40′ E) are comparatively small places, as is Arkhangel'skoye Kuroyedovo (53° 55′ N, 46° 58′ E), which is the place from which Witt (1886) had the material which is labelled 'Archangelsk', and these can be regarded as reasonably precise localities. On the other hand Simbirsk, now Ulyanovsk (54° 24′ N, 48° 24′ E), is a large town that gives its name to an oblast and hence may indicate a general district rather than a precise locality. The material so labelled may well be that from Beklemishevo (53° 52′ N, 47° 25′ E) studied by Weisse (1855), the title of whose paper says that it is about diatoms from 'Gouvernment Simbirsk'. In our accounts of the distribution of species we have, however, listed specimens labelled 'Simbirsk' as coming from Ulyanovsk rather than Beklemishevo. Sysran, an even larger town, would also appear to have been used as an indication of a general region for there are slides in the collections of the British Museum (Natural History) labelled 'Syzran, Simbirsk' and 'Syzran (Ananino)'. It accordingly seems very likely that all the specimens labelled 'Syzran' came from outcrops in Ulyanovsk oblast. Glezer (in Glezer et al., 1974: 109) concludes that all this material is of Paleocene age.

We have also examined specimens labelled as from 'Singiliewsky' or 'Singilievsky', another sample of fossil material received by diatomists in western Europe during the 1930s. There is no place with this name in the U.S.S.R. According to Reinhold (1945), this is an error for Sengilei (53° 58′ N, 48° 46′ E) in Ulyanovsk oblast. Glezer (in Glezer et al., 1974: 133–4) discusses the age of the diatom-bearing strata exposed at Sengilei but does not assign them firmly to the Paleocene or the lower Eocene, although she suggests that the diatom flora indicates a lower Eocene rather than a Paleocene date, and this we have adopted here.

Penza Oblast

Various fossil diatoms from an outcrop of Kuznetsk in Penza oblast were described by Pantocsek (1889), and we deal here with four from that locality. Pantocsek said that this material was of Triassic age, but this is certainly not the case. Jousé (in Proshkina-Lavrenko et al., 1949*a*) considered that the diatom flora from this locality is of Paleocene or lower Eocene age, but Glezer (in Glezer et al., 1974) concludes that it probably comes from the upper Eocene, as

Deflandre (1950) suggested on the basis of the silicoflagellates in the material, and we accept that date here.

We also found a specimen of *Briggera monoligata* R. Ross & P. A. Sims in a sample received from Mr Brigger and labelled 'Penza. Lower Eocene'. As this came from Dr Jousé, we think it probable that it is either from the basin of the river Chasa, a right-hand tributary of the river Sura in the Kuznetsk region, or from the basin of the river Davydovka, a right-hand tributary of the river Kanadeika, both in Penza oblast. Jousé (in Proshkina-Lavrenko et al., 1949*a*: 126–127) investigated the diatom flora from both these localities. Glezer (in Glezer et al., 1974) points out that this material is of lower Eocene age.

Voronezh oblast

Jousé (in Proshkina-Lavrenko et al., 1949*b*) illustrates a specimen of *Dicladiopsis* under the name *Keratophora robusta* from the Paleocene of Voronezh oblast, without giving a locality. According to Glezer (in Glezer et al., 1974), however, the deposits in Voronezh oblast are of upper Eocene age. Jousé (1955) also records *Kittonia granulata* Chenev. (a synonym of *Keratophora nitida* Pant.) from the lower Oligocene of Pavlodar, without stating the oblast in which this locality is situated. The largest place of that name is in north-eastern Kazakhstan, whereas it is only in the south-west of Kazakhstan that Paleogene deposits containing diatoms have been found (Glezer in Glezer et al., 1974). We therefore think it probable that Jousé was referring to the smaller settlement of the same name at 51° 43′ N, 42° 05′ E in Voronezh oblast, and that the correct date for this record is upper Eocene.

Voroshilovgrad oblast

Jousé (in Proshkina-Lavrenko et al., 1949*b*) also illustrates a specimen of *Dicladiopsis*, again under the name *Keratophora robusta*, from Staroverovka, Voroshilovgrad oblast, giving Oligocene as its age. However, Glezer, Zosimovich & Klyushnikov (1965) state that the material from which this specimen came is upper Eocene in age.

'Carlovo'

This is the locality name of another sample of diatom-bearing material from the U.S.S.R. that came into the hands of diatomists in western Europe in the 1930s. As is pointed out above, the locality names of two other such samples, 'Kamichev' and 'Singiliewsky', were almost certainly misspelled. There is only one place in the U.S.S.R. called Karlovo, a very small settlement in Tula oblast, 53° 44′ N, 36° 04′ E, some 250 km SSW of Moscow, in a region where no Paleogene diatoms are recorded by Glezer (in Glezer et al., 1974). It seems possible that 'Carlovo' is an error for Karlovka, the name of some 20 settlements in the U.S.S.R. One of these, at 53° 23′ N, 48° 59′ E, is in Kuibyshev oblast, and is only some 40 km SSE of Sengilei. Five others, at 47° 35′ N, 37° 27′ E, in Donetsk oblast, 48° 32′ N, 37° 57′ E, and 48° 57′ N, 34° 21′ E, in Dnepropetrovsk oblast, 49° 46′ N, 35° 56′ E, in Khar'kov oblast and 51° 51′ N, 41° 02′ E, in Tambov oblast are in the general area of the upper Eocene diatom-bearing deposits in the south-west of the European part of the U.S.S.R. (Glezer in Glezer et al., 1974). We have no information on the general diatom content of the sample from 'Carlovo' but have seen specimens of *Briggera includens* (Grunow) R. Ross & P. A. Sims and *Keratophora nitida* Pant. from there. The youngest firmly dated record of *B. includens* is from the lower Eocene, whilst *K. nitida* is known only from middle and upper Eocene deposits. We have some doubts, however, about the provenance of the specimen of *K. nitida*, which is the single specimen on a selected slide (BM 36231) prepared by S. H. Meakin, some of whose samples were contaminated. He had material from 'Kamichev', in which *K. nitida* is not uncommon, and this specimen may have been a stray from that material. The specimen of *B. includens* from 'Carlovo' was amongst those selected by Mr Brigger, and we would not regard the existence of the one particular specimen of *K. nitida* labelled as from the same locality as conclusive proof that the two species were contemporary. We accordingly incline to the view that 'Carlovo' is probably an error for the Karlovka in Kuibyshev oblast and that the material from there is of Paleocene or lower Eocene date and does not contain *K. nitida*.

Rostov

Another sample received from Mr Brigger is labelled 'Rostov. Upper Eocene', with no further information available about it. We have no means of telling whether this comes from Rostov-na-Donu, 47° 15′ N, 39° 35′ E, or from the Rostov at 52° 37′ N, 28° 44′ E, or from that at 57° 11′ N, 39° 25′ E, but, in the light of the information given by Glezer (in Glezer et al., 1974) about the places in the south-west of the European part of the U.S.S.R. where Eocene diatoms have been found, the first of these three is the most probable and the last the least.

Kaliningrad oblast
Strel'nikova, Kaplan & Travina (1978) record *Hemiaulus includens* Grunow (*Briggera includens* (Grunow) R. Ross & P. A. Sims) from a well at Prionersk in Kaliningrad oblast in material that they date as lower Eocene in age.

Barents Sea

Grunow (1884) described diatoms from a sample dredged from a depth of 100–500 m in the Barents Sea south of Franz-Josefs Land. He suggested no age for this material, but Reinhold (1945) pointed out that the diatom flora shows that it contained material of Paleocene to lower Eocene age, which he suggested was re-deposited after erosion from coastal deposits. However, material of this age may have been exposed on the sea bed. A more precise dating is not possible.

Poland

Schulz (1935) described the diatom flora from an outcrop on the shores of Zatoka Gdanska (the Gulf of Danzig), which he dated as Senonian (upper Cretaceous). No more detailed information about the age of this material is available.

Germany

One of the records that we give for *Briggera includens* (Grunow) R. Ross & P. A. Sims is based on a specimen illustrated as *Hemiaulus* sp. by Benda (1965), who was reporting on the diatom flora of a deposit of Ypresian (lower Eocene) age from the Isle of Fehmarn in the south-western Baltic between the Kieler Bucht and the Mecklenburger Bucht.

Czechoslovakia

We found a new species of *Briggera* in material from Pausram, now Pouzdřany, Czechoslovakia, 48° 56′ N, 16° 37′ E; Pantocsek (1909) described *Aulacodiscus gutwinskii* from this locality. According to Reháková (personal communication) the outcrop of diatomaceous sediment at Pouzdřany is of Aquitanian (lower Miocene) age.

U.S.A.

The sample from the Moreno shale that has been studied by diatomists comes from Moreno Gulch, 36° 44′ N, 121° 44′ W, in the north-west of Fresno County, California (Anderson & Pack, 1915; Hanna, 1927). This material is of Maastrichtian (upper Cretaceous) age (Popenoe, Imlay & Murphy, 1960).

North Atlantic

Oceanographer Canyon, 40° 30′ N, 68° 10′ W
A specimen of *Briggera includens* (Grunow) R. Ross & P. A. Sims from dredge sample D 25 was shown to one of us (R.R.) by Dr Juliane Fenner. The only information available to her about this material was that it came from the Oceanographer Canyon from a depth between 1510 m and 978 m and that Dr G. Blechschmidt (unpubl.) had dated the sample as upper Turonian-Coniacian on the basis of calcareous nannofossils.

Bermuda Rise
Specimens received from Mr Brigger include some labelled 'Bermuda Rise'. These come from Deep Sea Drilling Project, Leg 1, Site 6, 30° 50·39′ N, 67° 38·86′ W. Mr Brigger had a number of samples from core 4 taken at this site but there is no indication of the particular level in the core

from which these specimens come; however, the whole of this core comes from the middle Eocene (Initial Rep. deep sea Drilling Proj. 1: 243–292. 1969).

Barbados

The fossil diatoms found in this island occur in the Oceanic Beds, which range in age from the middle Eocene to the lower Miocene. Kugler (1961) gave an age range for them of upper Eocene to lower Miocene, but more recently some samples from them have been dated as middle Eocene by their radiolaria (Holmes & Brigger, 1979), and the same age has been found for the base of a section at Bath Cliff, Conset Bay (Saunders et al., 1983). Apart from some specimens labelled simply 'Barbados', for which no precise dating is possible, we have specimens or records from the following localities on the island:

Cambridge

Two of Greville's slides from Cambridge have on them specimens that have been dated as middle Eocene on the basis of the radiolaria also present (Holmes & Brigger, 1979). As all the specimens from Cambridge that we have seen are on slides prepared by Greville, we have assumed that they are all of middle Eocene age.

Chalky Mount

There is no published information about the sediments containing diatoms from this locality, which lies about 1 km NW of Cambridge.

Conset

A sample from this locality, almost certainly the one from which our specimens came, has been dated as early middle Eocene by W. R. Riedel on the basis of its radiolaria (Holmes & Brigger, 1979). Our specimens came from material received from Mr Brigger, who had it from Mr J. H. Robinson. The details of the exact locality have been given by Robinson (1936*a*). The other localities where there occur diatoms found in the sample from Conset studied by Holmes and Brigger raise doubts, however, about the accuracy of this age determination. They found four taxa of *Entogonia* from there but, in all cases, not from any other locality in Barbados. Three of these, *E. formosa* (Truan & Witt) Bergon var. *formosa, E. jeremiana* Bergon var. *jeremiana*, and *E. jeremiana* var. *pentagona* (Truan & Witt) Bergon, also occur in the deposit of Jérémie, Haiti, for which Holmes & Brigger (1979) give an early Miocene date based on radiolaria, and two, *E. formosa* var. *formosa* and *E. formosa* var. *protuberans* Holmes & Brigger, also occur in Reinhold's (1937) sample AY 12 from Java, which he dates as middle Miocene. Also, the one specimen from Conset with which we are concerned belongs to a species, *Briggera haitensis* (R. Ross) R. Ross & P. A. Sims, known otherwise only from Jérémie, Haiti. This suggests that the sample from Conset containing these *Entogonia* specimens and *Briggera haitensis* is much closer in age to those from Jérémie and Java than the ages given by Holmes & Brigger (1979) suggest. The observations of Saunders et al. (1983) show that there is a continuous section from middle Eocene to lower Oligocene exposed at Bath Cliff, Conset Bay, and there is a thus a possibility that the sample from which these specimens came is of a different and later date than that dated by radiolaria. The sample collected by Robinson came from further inland than Bath Cliff and so might by even later than lower Oligocene. Again, not very much is known about the exposures at Jérémie, Haiti, and they too may cover a considerable age range. However, unless Reinhold's (1937) determination of the age of his sample AY12 from Java is widely inaccurate, it seems probable that the sample from Conset with which we are concerned here is later than middle Eocene. There must also be some uncertainty about the early Miocene date for the material from Jérémie, Haiti.

Joe's River

A sample from this locality has been dated as coming from the Eocene–Oligocene boundary (Holmes & Brigger, 1979). As our one record from this locality is based on a specimen mounted by Mr Brigger, we assume that it comes from this sample. Topographical details of the place from which it came are given by Robinson (1938).

Mount Hillaby
There is no published information about the sediments containing diatoms from this locality.

Newcastle
One of the two specimens from this locality is labelled simply 'Newcastle' and comes from material collected in the nineteenth century. The other is from Clarke's Cliff, Newcastle, from the outcrop described by Robinson (1936*b*). There is no published information about the geological age of either of these samples, but their diatom flora suggests a later date than that of the material from Cambridge; they are probably no earlier than upper Eocene and may be appreciably later.

Haiti

Truan & Witt (1888) described the diatom flora from samples taken from the top of the cliffs on either side of the town of Jérémie in the south-west of Haiti. A sample from that locality believed to be part of their original material has been dated as early Miocene by W. R. Riedel on the basis of the radiolaria contained in it (Holmes & Brigger, 1979). We have, however some reservations about this dating for reasons discussed under Conset, Barbados, above (p. 283).

South Atlantic

São Paulo plateau
Fenner (1977: pl. 31 fig. 13, 14) illustrates a diatom that we identify as *Briggera capitata* (Grev.) R. Ross & P. A. Sims. This comes from middle Eocene material from Deep Sea Drilling Project Leg 39, site 356, 28° 17·22′ S, 41° 05·28′ W on the south-eastern part of the São Paulo plateau.

Falklands plateau
Specimens cited in this paper come from the following samples from cores taken by R/V Vema; we are indebted to Dr Juliane Fenner for determinations of the ages of these.

Vema cruise 12, core 46, 47° 28·7′ S, 59° 20·6′ W, 630 cm from top of core; middle Eocene with strong admixture of re-worked Paleocene and lower Eocene material.

Vema cruise 17, core 107, 51° 08′ S, 54° 22′ W, 50 cm and 120 cm from top of core; both samples middle Eocene.

Vema cruise 18, core 104, 53° 01′ S, 52° 52′ W, 330 cm from top of core; middle–upper Eocene.

Descriptions of the sections from which these came are given by Hanna, Hendey & Brigger (1976) and by Ross (1976). There is also one record from a core taken by R/V Conrad of which the details are:

Conrad cruise 12, core 237, 47° 45·7′ S, 57° 38·5′ W.

This material is said to be of Eocene date, but we have no further information about it.

Indian Ocean

One of our records is based on a specimen from a dredge sample (Dodo–123–D1) collected on the expedition Dodo of the Scripps Institution of Oceanography at 10° 25′ S, 63° 15′ E, from a depth of 3115 m. This sample has been dated as coming from the middle–upper Eocene boundary (Holmes & Brigger, 1977).

New Zealand

Many specimens of two species considered here come from the diatomite exposed at Oamaru, Otago Province, New Zealand. The Waiareka Volcanic formation, in which this material occurs, is of upper Eocene age (Gage, 1957). Whilst the locality given for many of the specimens does not specify the outcrop from which they came, this information is given for others, the outcrops from which there are specimens recorded by us being: Allan's Farm, Bain's Farm, Borries, Cave Valley, Cormack's Siding, Dick's Farm, Forrester's Hill, Jackson's Paddock, Jackson's Well, Papakaiyo, Railway Cutting, Totara, Troublesome Gulley, and William's Bluff. Topographical details of most of these are given by Doig (1962, 1967).

Taxonomic account

Terminology

In the descriptions of taxa in this account the terminology suggested in Anon. (1975) and Ross et al. (1979) is adopted, but there are some additional terms used here which need to be defined. The valves of many of the species dealt with consist of three parts more or less sharply delimited from one another: a central portion and two portions, one on either side of this, each of which may be longer, i.e. extend further along the apical axis, than the central portion. One example of a species with a valve of this shape is *Briggera includens* (Grunow) R. Ross & P. A. Sims (Pl. 1 fig. 6). It is clearly not satisfactory to call these distal portions of the valve 'apices' as various authors, e.g. Wise (1952), have done; that term is required for their tips. In the earlier treatment by one of us (Ross, 1972) of species here included in our new genus *Briggera*, these parts of the valve were referred to as 'terminal portions', but the very considerable number of species in diverse genera with valves with a shape of this sort makes it desirable to replace this by a term consisting of a single word. We accordingly propose, and use here, the term 'projection' (Latin: projectura) for the distal parts of the valves where these are distinguishable as entities, but retain 'central portion' (Latin: portio centralis) for the part of the valve between the projections. It is, of course, not only in bipolar diatoms that projections occur; they are also to be found in tripolar and multipolar species, e.g. *Triceratium trisulcum* Bail. (see Schmidt, 1886: taf. 112 fig. 17) and *Trinacria exsculpta* (Heib.) Hust. (see Ross, Sims & Hasle, 1977: pl. 9 fig. 57). These projections are not always as distinct from the central portion of the valve as they are in such species as *Briggera includens*; in many species, e.g. *Strelnikovia antiqua* (Streln.) R. Ross & P. A. Sims (Pl. 20 fig. 1,2), the central portion tapers into the projections. All the species with projections that are dealt with in this paper have elevations on the projections close to their apices.

There is a pattern of arrangement of the areolae which occurs in a number of species of the Biddulphiaceae, including several of those dealt with in this paper, and which is more common in the Eupodiscaceae. The areolae occur some singly, and some in rows of varying length, but all of them so positioned that they fall on a pattern of radial lines. The extent to which this pattern is interrupted by gaps can vary considerably from specimen to specimen within the species, and also in different parts of the same valve, the gaps in the radial rows usually being fewer towards the margin. This pattern we term 'Areolae in interrupted radial rows'.

We also use the term 'sibling valve', which does not appear in Ross et al. (1979) but was introduced by Fryxell & Miller (1978), who considered its meaning sufficiently obvious for it not to need definition (Fryxell, personal communication). 'Sibling' is, however, not a word in very common use and a definition seems desirable. The hypovalves of two daughter cells formed simultaneously within the girdle of a mother cell are 'sibling valves'. In almost all the species dealt with in this paper, pairs of sibling valves are held together by linking spines that have their upper parts broader than their bases and thus interlock; in consequence the frustules are in chains and can separate only if the linking spines are broken. Following von Stosch (1977) we speak of colonies in which separation of the cells entails breaking of the valves as 'inseperable'.

We describe the frustules of all the genera dealt with here as 'rectangular'. By this we mean that a figure with four sides enclosing the frustule as seen in girdle view is a rectangle because the two elevations on each valve are of equal height, so that a chain of frustules is straight. This is in contrast to the situation in such species as *Hemiaulus elegans* (Heib.) Grunow, where the two elevations are of different heights and the chain of frustules is curved (see Ross, Sims & Hasle, 1977: pl. 7 fig. 46).

In many of the species one of each pair of sibling valves has a circumferential step on its mantle similar to that reported by Crawford (1982) in *Melosira arenaria* Moore ex Ralfs. He showed that in that species the step occurs at the free edge of the hypocingulum of the mother cell and this is presumably also the case in the species described here. The species in which we have observed this step, which might, we suggest, be called the 'Crawford step', are: *Briggera includens, B. morenoensis, B. siberica, B. monoligata, B. capitata, B. vemae, B. affixa, B. ornithocephala* subsp. *atlantica, B. bonei, Strelnikovia antiqua,* and *Keratophora nitida,* but in *B. ornithocephala* subsp. *atlantica* and *K. nitida* it is present in some cases but not in others. On the other hand, we have observed in *Briggera ornithocephala* subsp. *ornithocephala*, *B. haitensis*, and *Strelnikovia auliscoformis* pairs of sibling valves in which neither has such a step. Its absence in these species is presumably due to the wide separation of the mantles of a pair of sibling valves because of the height of the elevations, with the result that the free edge of the hypocingulum of the mother cell falls between them. We have not repeated the information given above about the occurrence of the Crawford step in our descriptions of the individual species.

The genera

The five genera that we deal with in this paper all have valves with two elevations that are swollen above, but they differ from all the other genera in which this feature occurs by the simultaneous presence of two characters. On the summits of their elevations they have linking spines that interlock inseparably because they are broader above than below; one of the 15 species of *Briggera, B. ornithocephala* (Grev.) R. Ross & P. A. Sims, is a partial exception in that its linking spines, which are never much expanded above, occasionally do not expand at all, so that the frustules are not inseparable. Also, on the distal sides of the tips of their elevations, and often extending on to their summits, there are pseudocelli with indefinite margins, i.e. the areolae become more widely spaced towards the margins of the pseudocelli, so that these have no definite margins. There are very few other genera with similar interlocking spines borne on elevations. They occur in *Trinacria exsculpta* (Heib.) Hust., a species misplaced in that genus, but this has a comparatively small pseudocellus with a much more definite margin; also its elevations are not swollen above (see Ross, Sims & Hasle, 1977: pl. 9 fig. 60). The elevations of *Pseudorutilaria* Grove & Sturt are very similar to those of *Trinacria exsculpta* (Ross & Sims, personal observation). Interlocking spines also occur in *Hemiaulus centralitenuis* R. Ross & P. A. Sims but in this species too there is a very small pseudocellus with a definite margin (see Ross, Sims & Hasle, 1977: pl. 2 fig. 8). We now consider that this species is not congeneric with the type species of *Hemiaulus* Heib., nom. cons. prop. The interlocking spines of *Dextradonator* R. Ross & P. A. Sims are quite different from those of the genera discussed here, that genus having only a single forked linking spine on each elevation; moreover, it has no large pseudocelli (see Ross & Sims, 1980: pl. 1 fig. 3).

In *Briggera* R. Ross & P. A. Sims, the number of linking spines is usually less than six, never more. These linking spines are borne on the proximal side of the summit of the elevation; they are triangular in section at the base, with the apex of the triangle pointing towards the centre of the elevation, and the upper part is crescentic in section with the convex side of the crescent towards the centre of the elevation. In all the species the valve is crossed by two sulci or, more rarely, four, which may be quite shallow to very deep. There are 15 species in this genus, seven of them previously undescribed. The other eight have all been included until now in *Hemiaulus* Heib.; however, the type species of that genus and most of the others included in it differ from *Briggera* in many ways. Their linking spines taper upwards and do not interlock, their elevations are more slender and are not expanded above, their pseudocelli are much smaller or almost non-existent, they have no transverse sulci although transverse internal costae are often present, and their areolae are in general larger and more closely spaced than those of *Briggera* and are without a marginal rim. These many differences are a more than sufficient basis for separating from *Hemiaulus* the species which we include here in *Briggera*.

Whilst the evidence is not conclusive, it would seem that in *Dicladiopsis* De Toni the frustules are always heterovalvar, one of the two valves of each frustule having linking spines at the summits of its elevations whilst the other does not. The elevations of the valves with linking spines are very similar to those of *Briggera*: the tips are expanded, each with three to four interlocking linking spines on the proximal side and a pseudocellus with indefinite margins on the distal side. The valves without linking spines have rounded tips to their elevations bearing large pseudocelli with indefinite margins. In this genus the valves have no transverse sulci, and this enables one to recognize that valves with linking spines when found separately belong to this genus and not to *Briggera*.

Strelnikovia R. Ross & P. A. Sims has many more linking spines than *Briggera* and they are somewhat different in shape. Their bases are narrowly elliptical or linear in cross section, the long axis pointing towards the centre of the elevation, and in side view they have approximately the shape of a right-angled triangle, the right angle being at the outer end of the base. The linking spines form a band along the lateral and proximal sides of the summits of the elevations, in one species almost surrounding these but with a small gap on the distal side. In some species the elevations rise very little above the general level of the valve. Sulci are present in only one species, *S. incerta* R. Ross & P. A. Sims. Two of the previously known species were placed in *Rutilaria* Grev. and two in *Biddulphia* Gray, but their lack of a periplekton and of true ocelli separates them from the former and the presence of linking spines from the latter.

The linking spines of *Keratophora* Pant. are very similar to those of *Strelnikovia* but they form a complete ring around the summits of the elevations. The elevations arise from rounded hyaline transverse ridges or from hyaline areas of the valve, and they themselves are hyaline, except for their pseudocelli, tubular and usually sinous; in all these respects they differ from *Strelnikovia*.

Thaumatonema Grev. has elevations and linking spines very similar to those of *Keratophora* but these arise from a boss or common vertical tube at the centre of the valve. The genus also differs from all those already discussed in having circular or almost circular valves and loculate, not poroid, areolae. However, its interlocking linking spines and its pseudocelli show that it should be grouped with them.

The five genera discussed above, *Briggera, Dicladiopsis, Strelnikovia, Keratophora,* and *Thaumatonema*, are clearly closely related to one another, much more so than they are to any others with linking spines, and they could well be regarded as constituting a tribe within the subfamily Hemiauloideae. However, it would not be appropriate to establish a tribe for these genera except in the context of a tribal classification of the whole subfamily, or rather of the whole family Biddulphiaceae, for there are reasons discussed below (p. 340) for questioning its subdivision into Biddulphioideae and Hemiauloideae. Were such a classification to include a taxon comprising these five genera, its diagnostic characters would be: bipolar valves with elevations bearing linking spines narrower below than above and thus interlocking, and well developed pseudocelli with indefinite margins. The following is a conspectus of the genera of the Biddulphiaceae with these characteristics:

Briggera R. Ross & P. A. Sims – frustules not normally heterovalvar; valves crossed by two sulci or more; elevations arising at or close to the apices of the valve, not from transverse ridges across the valve or hyaline areas; linking spines six or fewer on the proximal side of the summit of each elevation, triangular in cross section at their base, in their upper part crescentic in cross section and concave on their outer side.

Dicladiopsis De Toni – frustules normally heterovalvar with only one valve with linking spines; valves not crossed by sulci; elevations arising at or close to the apices of the valve or more centrally, not from transverse ridges across the valve or from hyaline areas; linking spines six or fewer on the proximal side of the summit of each elevation, triangular in cross section at their base, in their upper part crescentic in cross section and concave on their outer side.

Strelnikovia R. Ross & P. A. Sims – frustules not normally heterovalvar; valves crossed by two sulci or none; elevations arising at or close to the apices of the valve, not from transverse ridges across the valve or hyaline areas, not tubular; linking spines 12 or more, surrounding the summit of each elevation except for a gap on the distal side, elliptical to almost linear at their bases, and triangular in side view.

Keratophora Pant. – frustules not normally heterovalvar; valves not crossed by sulci; elevations arising considerably proximal to the apices from rounded transverse hyaline ridges or from hyaline areas, tubular; linking spines many, completely surrounding the summit of each elevation, almost linear at their bases and triangular in side view.

Thaumatonema Grev. – frustules not normally heterovalvar; valves not crossed by sulci; elevations arising from a circular hyaline area in the centre of the valve, their lower parts sometimes fused to form a single vertical tube, tubular; linking spines many, completely surrounding the summit of each elevation, almost linear at their bases and triangular in side view.

All the genera of this group are entirely fossil and, except for one, or possibly two, species of *Briggera*, and also possibly one species of *Thaumatonema*, they are confined to the upper Cretaceous and the Paleogene; those that do or may occur later are not found above the lower Miocene. Both *Briggera* and *Strelnikovia* are found in the upper Cretaceous, with *Briggera* persisting until the lower Miocene and *Strelnikovia* until the upper Eocene. *Dicladiopsis* and *Keratophora* are known only from the Eocene, and *Thaumatonema*, the earliest known occurrence of which is in the middle Eocene, may extend into the Oligocene, or, just possibly, into the lower Miocene; one of the samples from the Oceanic Beds of Barbados in which it has been found is of unknown position within these beds.

Separation valves

Except for the species of *Dicladiopsis* in which the frustules are apparently united in inseparable pairs, all the diatoms considered in this paper form inseparable filamentous colonies; their frustules are joined in a chain by the interlocking linking spines of sibling valves. One can assume, however, that these chains are of finite length. There will thus be a proportion of cell divisions in which the sibling valves are not united by interlocking linking spines. The colonies have always been fragmented during fossilization and even single whole frustules are uncommon; when they do occur they are almost always very recently divided cells which have not yet formed hypocingula. Most of the specimens are either single valves with broken linking spines or pairs of sibling valves held together by their interlocking linking spines. In consequence, we have no certain knowledge of the extent to which the separation valves differ from those within the chain.

The problem is much increased by the fact that the only character that separates some species of *Biddulphia* Gray from the species of *Briggera* with sharply delimited projections is the absence of linking spines. Also, there are some undescribed species that are very close to *Strelnikovia* in all other respects but lack linking spines. These, too, would be regarded as belonging to *Biddulphia* by most authors, although they fall outside the limits of the genus put forward by Hendey & Sims (1984). On the other hand, the elevations of *Keratophora* and *Thaumatonema* are so distinctive that separation valves of these genera would be recognisable as belonging to them provided that they were not without elevations as well as interlocking linking spines; if they did lack elevations, the end cells of *Keratophora* would probably be identified as *Anaulus* and those of *Thaumatonema* as *Coscinodiscus*. We have, however, found valves of *Keratophora nitida* Pant., the sole species of the genus, with unusually tall elevations and apparently vestigial linking spines, which we consider to be separation valves of that species. These are discussed in more detail in our account of the species (p. 335).

In *Briggera* the situation is more complex. We have found a few specimens from the upper Eocene deposits at Oamaru, New Zealand, in which *B. capitata* (Grev.) R. Ross & P. A. Sims occurs in some numbers, that resemble that species exactly in all characters except that they lack linking spines. The type specimen of *B. capitata* is also without linking spines and it is identical to the specimens from Oamaru. However, it occurs in the middle Eocene of Barbados and is the only specimen, with or without linking spines, to have been found there. We nevertheless consider that it is a separation valve of the species that occurs in the Oamaru deposits as this is how we interpret the identical specimens from those deposits. It is for this reason that we apply the name *Briggera capitata* to this species, just as one of us earlier (Ross, 1972) called it *Hemiaulus capitatus* Grev. In this we differ from Wise (1952), who considered that the type specimen of *H. capitatus* belonged to the genus *Biddulphia*.

All that definitely distinguishes *Biddulphia novae-zealandiae* Wise (1952) from *Briggera includens* (Grunow) R. Ross & P. A. Sims is the lack of linking spines, although there may also be a slight difference in the outline of the valve, the projections in *Biddulphia novae-zealandiae* being a little less narrowed proximally and also somewhat more cuneate at the apices. However, *Biddulphia novae-zealandiae* occurs in the upper Eocene of Oamaru, New Zealand and, although it is rare there, a number of specimens of it have been found. However, no specimens of *Briggera includens* with linking spines have been found in the Oamaru material, and the species is not known from any deposits of later age than the lower Eocene, unless the material from 'Carlovo' is younger than this (see p. 281), nor does it occur outside the northern Atlantic, northern and eastern Europe, and the western fringe of Siberia. For this reason we consider that *Biddulphia novae-zealandiae* is a separate species and correctly placed in that genus. Specimens indistinguishable from those of Oamaru occur very rarely in the upper Eocene deposits from Kuznetsk and 'Kamichev' (see p. 280) in the U.S.S.R., again as members of a flora that does not contain *Briggera includens*, and these also we identify as *Biddulphia novae-zealandiae*. The specimen from Kuznetsk (BM coll. Adams M89) was identified earlier as *Hemiaulus includens* (Ross, 1972) but this we now consider to be an error.

In the Paleocene material from Simbirsk (now Ulyanovsk), U.S.S.R., in which *Briggera includens* is not rare, we have found a single valve (Pl. 30 fig. 1) that differs from *Biddulphia novae-zealandiae* by having its projections more narrowed proximally and rounded, not cuneate, distally. It thus has an outline that falls well within the range of *Briggera includens*, from which it differs only in its lack of linking spines. Is it a separation valve of that species or a specimen of *Biddulphia* sp. closely related to *B. novae-zealandiae*? There is no firm evidence to help one decide one way or the other, but the fact that it is much rarer in this material than *Briggera includens* with linking spines, and its very close resemblance to it, incline us to the view that it is a separation valve of that species. We have also found an almost identical specimen from 'Carlovo' (for this locality see p. 281 above), where *B. includens* with linking spines also occurs. This specimen is illustrated as Pl. 30 fig. 2.

Briggera includens also occurs in the Campanian (upper Cretaceous) of the eastern Urals. In the deposits from that region there are two species that are similar to *Biddulphia novae-zealandiae* and to the specimens from Simbirsk and 'Carlovo' that are, we suggest, separation valves of *Briggera includens* but differ sufficiently to be clearly distinct from either and from each other. One (Pl. 30 fig. 4) has broader valves than *Biddulphia novae-zealandiae* and *Briggera includens* and also differs from these two species by having a marginal ridge on either side that extends from one elevation to the other and areolae on the mantle opposite the central portion of the valve. In *Biddulphia novae-zealandiae* and *Briggera includens* the marginal ridge is not continuous across the central portion of the valve and there are no areolae on the mantle opposite it. In the other species (Pl. 30 fig. 3), which was confused by Strel'nikova (1974) with *Briggera includens* and is discussed more fully in our account of that species below (p. 297), the marginal ridge is interrupted opposite the central portion of the valve, but there are areolae on the upper portion of the mantle there and the projections are much narrower than in *Briggera includens*.

The existence of species such as these two from the Campanian of the eastern Ural mountains and *Biddulphia novae-zealandiae* which are sufficiently similar to *Briggera* to be confused with it means that the identification of single valves without linking spines as separation valves of *Briggera* spp. can only be tentative in the present state of our knowledge and some uncertainty must remain about the way in which we apply the name *Briggera capitata*.

In the Campanian deposits from the eastern Ural mountains, both from those exposed near Til'tim and from those recovered from cores taken near Ust'-Man'ya, there are specimens without any trace of linking spines that bear a close resemblance to *Strelnikovia auliscoformis* (Streln.) R. Ross & P. A. Sims and *S. inclinata* R. Ross & P. A. Sims. These specimens (Pl. 30 figs 5–8), which belong to at least two different species, more probably three, resemble these two species of *Strelnikovia* in the outline and contour of their valves, the shape and size of their elevations, and the size, distribution and spacing of their areolae. There are, however, differences in detail that would separate them from these species even if they possessed linking spines. Instead they all have elevations that are rounded above with the rounded summits covered by pseudocelli. These specimens, although not very common, are more frequent in the material than those with linking spines that they resemble. The likeness is so great that it is difficult to believe that they do not have a close relationship with *Strelnikovia*, but the nature of that relationship is an enigma. We discuss it further below (p. 000) when considering the relationships of this group of genera to the remainder of the Biddulphiaceae.

Labiate processes

In the Biddulphiaceae, in which the labiate processes can be very close to, or even on, the mantle of the valve, one can only be reasonably certain of detecting them if one can examine with the scanning electron microscope a valve mounted with its inner side uppermost, and in valves with deep mantles it can even then be extremely difficult to be certain whether or not any are present. Because of the limited number of specimens of many species available to us, we have in many cases not been able to mount one in this position. We have therefore said 'no labiate process seen' rather than 'without any labiate process' in our descriptions of those species where we have not detected one. All the labiate processes that we have seen are of the sort normal in the Biddulphiaceae, their inner opening being a comparatively short, straight slit across a semi-ellipsoidal raised portion of the inner surface of the valve, and their outer portion a straight tube.

All the species of *Briggera* in which we have seen labiate processes belong to the group with sharply delimited projections. We have been able to examine with the scanning electron microscope the interior of three species with elliptical valves, *B. ornithocephala* (Grev.) R. Ross & P. A. Sims, *B. bonei* R. Ross & P. A. Sims, and *B. haitensis* (R. Ross) R. Ross & P. A. Sims, but have seen no labiate processes in any of these. It would thus seem probable that there is a real difference in this respect between these groups within the genus.

In *Strelnikovia* we have found labiate processes in two species, *S. antiqua* (Streln.) R. Ross & P. A. Sims and *S. incerta* R. Ross & P. A. Sims, but not in a third, *S. auliscoformis* (Streln.) R. Ross & P. A. Sims, in which we were able to examine the interior of a valve with the scanning electron microscope. It is interesting that in this genus also labiate processes are present in the species with elongate valves but are apparently absent in one with broadly elliptical valves.

We have seen no labiate process in any of the other three genera, but it is only in *Keratophora nitida* Pant., the sole species of that genus, that we have been able adequately to examine the interior of a valve with the scanning electron microscope.

Vela

As is so frequently the case with fossil specimens, the vela are missing, lost by erosion, from almost all the specimens we have examined; in only two, of different species, are those of the normal areolae intact, and in only six more are there vestiges; in addition there is one species with vela visible in the areolae of the pseudocellus but not elsewhere. Thus, of the 30 species we describe in this paper, we have no information about the vela of 21, in six cases because we have been able to examine specimens only with the light microscope but in 15 because there were no traces of vela in the specimens that we examined with the scanning electron microscope. For this reason we have not included such data as are available about them in the descriptions of the species but instead present it here.

In *Keratophora nitida* Pant. the vela consist of rotae with two to six arms and a circular central disc sometimes pierced by one to three small circular holes (Pl. 28 fig. 4). The space between the arms of the rotae is almost completely filled by a vola-like occlusion attached to the central disc, with the result that the only openings through the velum, other than the holes through the central disc, are a series of narrow slits about three quarters of the circumference of a circle in shape. Occasional areolae smaller than the others and only *c.* 0·25 μm in diameter, are occluded by a single vola.

The vela of *Strelnikovia antiqua* (Streln.) R. Ross & P. A. Sims are also rotae; they have up to five arms, three being the usual number (Pl. 21 fig. 6). The arms of the rotae widen towards the margin of the areolae to such an extent that they fuse, the outer edge of the hole between each pair being a segment of a circle. The specimen of this species in which the areolae are preserved appears to be rather more eroded than that of *Keratophora nitida* with intact vela. It is thus possible that the openings in intact vela of *S. antiqua* may have been slits as narrow as those in *K.*

nitida. The vela of the areolae in the pseudocellus of *S. antiqua* are similar to those on the rest of the valve, except that their arms are narrower and, in many cases, there are only two of these (Pl. 20 fig. 4).

Whilst there are no vela visible in the sparse areolae on the valve surface of the one specimen of *Strelnikovia* sp. I that we have seen, the areolae of the pseudocellus are occluded either by rotae with two arms or by volae (Pl. 27 fig. 7).

In one specimen of *Strelnikovia incerta* R. Ross & P. A. Sims there are inwardly projecting pegs on the margins of some of the areolae (Pl. 26 fig. 6) that suggest that its vela when intact were very similar to those of *S. antiqua*.

The other five species in which there are some traces of vela all belong to the genus *Briggera*. In *B. includens* (Grunow) R. Ross & P. A. Sims there is a single peg projecting inwards from the margin of some areolae (Pl. 1 fig. 8), suggesting that these were occluded by volae. A moderately well preserved specimen of *B. morenoensis* R. Ross & P. A. Sims has rotae with three or four arms in some areolae (Pl. 2 fig. 4). Enough remains of the vela in some areolae of *B. capitata* (Grev.) R. Ross & P. A. Sims to show that they were rotae with two to five arms (Pl. 6 fig. 6). Some areolae of *B. bonei* R. Ross & P. A. Sims have two small projections on the inner side of their margins (Pl. 13 fig. 4) and some of *B. haitensis* (R. Ross) R. Ross & P. A. Sims have one to three small projections in the same place.

Thus, whilst we know nothing of the vela in most of the species with which we are concerned, all those for which we have any information apparently have rotae or volae. Reticulate cribra, which are probably the most common type of velum within the Biddulphiaceae, were not present, it would seem, in any of them. This may be connected with the small size of the areolae in many species, but in both *Briggera capitata* and *B. haitensis*, for which we have some information, the areolae are quite large, 1·0 μm or more in diameter.

Imperfectly known species

Amongst the specimens that we have examined with the scanning electron microscope, there is one of *Briggera*, two of *Dicladiopsis*, and one of *Strelnikovia* that clearly do not belong to any of the species of these represented by the other specimens that we have seen; the two specimens of *Dicladiopsis* are conspecific. A specimen on a stub prepared for scanning electron microscopy is not satisfactory as a type; its conservation is less well assured than that of one mounted for light microscopy. For this reason, and also because a single specimen is an inadequate basis for the description required to give valid publication to a new specific name, we have not published names for the three species the existence of which is attested by the occurrence of these specimens; instead we designate them *Briggera* sp. I, *Dicladiopsis* sp. I, and *Strelnikovia* sp. I, giving descriptions of them at the end of our treatment of those genera.

Citation of specimens

In the accounts of each species we cite all the specimens that we have seen, indicating the collections in which they are preserved by the acronyms given in *Index Herbariorum* (Holmgren, Keuken & Schofield, 1981), which can also be found in Fryxell (1975). We quote not only the specimens on microscope slides but also those we have examined with the scanning electron microscope, giving their serial numbers in the collection of scanning electron micrographs at BM.

I. ***BRIGGERA*** R. Ross & P. A. Sims, **gen. nov.**

Frustula in catenis rectis plerumque inseparabilibus conjuncta, axe pervalvari tam longa vel longiore quam apicali. Valvae bipolares, sulcis duobus vel pluribus, raro, in speciminibus minimis, uno, traversae, elevationibus duabus plerumque robustis et supra tumidis. Areolae poroides et, praeter eas in pseudocellis, distantes. Pseudocelli plerumque magni, marginibus indefinitis, ad partem distalem et nonnumquam ad verticem summi elevationum, interdum in partes duas area hyalina paene divisi. Spinae ligantes 5 vel pauciores, in marginem proximalem verticis elevationis insertae, plerumque supra expansae et implexae. Rimoportula nulla vel una usque ad 5 prope centrum valvae, interne non exstans, rimo recta, externe ex tubo recto curto constans. Utrumque cingulum ex 3–4, forsan pluribus, taeniis profundis apertis constans.

SPECIES TYPICA: *Briggera ornithocephala* (Grev.) R. Ross & P. A. Sims, comb. nov., infra (p. 309).

Frustules united in straight, usually inseparable chains, as deep as to much deeper than their apical length. Valves bipolar, crossed by two or more sulci, rarely, in very small specimens, by only one, with two elevations that are usually robust and swollen above. Areolae poroidal and, except for those of the pseudocelli, distant. Pseudocelli usually large, with indefinite margins, on the distal part and sometimes also the upper surface of the tips of the elevations, occasionally almost divided in two by a hyaline area. Linking spines 5 or fewer, inserted on the proximal edge of the summit of the elevations, usually expanded above and interlocking. Labiate process absent, or 1–5 near the centre of the valve, their internal part not projecting, their internal opening a straight slit, their external part a short tube. Each cingulum of 3–4, perhaps more, deep open bands.

This genus is named in honour of the late A. L. Brigger of Yucaipa, California, U.S.A., who provided much of the material used in this study and who, by his skill and patience in selecting and mounting specimens, contributed much to our knowledge of fossil diatoms.

Briggera ornithocephala is chosen as the type species of this genus as it was the first species to be described, it is not uncommon in the readily available fossil deposit from Oamaru, New Zealand, and there is no question about the application of the specific name; the type specimen is in the collection at BM.

All the species of this genus known until now have been treated as belonging to the genus *Hemiaulus* Heib. (nom. cons. prop.), although Greville (1865 *a, b*), when describing *H. ornithocephalus* and *H. capitatus*, was very doubtful whether they really belonged to that genus. *Hemiaulus*, however, has slender elevations that taper upwards, linking spines that do not expand above and interlock but slot together, and areolae that are, in most species, larger and more closely packed than those of *Briggera*; also well developed pseudocelli are not present in *Hemiaulus* (see Ross, Sims & Hasle, 1977, but note that *H. centralitenuis* R. Ross & P. A. Sims, not dealt with in this paper, does not belong in *Hemiaulus*).

The species of this genus fall into two groups. In one the species have valves having two projections sharply delimited from the central portion and separated from it by deep transverse sulci, although very small specimens of one of the species in this group can have valves that are almost elliptical. To this group belong: *Briggera includens* (Grunow) R. Ross & P. A. Sims, *B. morenoensis* R. Ross & P. A. Sims, *B. siberica* (Grunow) R. Ross & P. A. Sims, *B. monoligata* R. Ross & P. A. Sims, *B. capitata* (Grev.) R. Ross & P. A. Sims, *B. vemae* R. Ross & P. A. Sims, *B. affixa* (R. Ross) R. Ross & P. A. Sims, and *B. robusta* R. Ross & P. A. Sims. *B. caverna* (Brun) R. Ross & P. A. Sims, which differs in outline from these species but, like them, has a valve crossed by deep sulci, also belongs here. This group occurs in the oldest fossil material in which the genus is represented, the upper Turonian-Coniacian (upper Cretaceous) sample dredged from the Oceanographer Canyon, western North Atlantic. The second group consists of species with elliptical to sub-circular valves crossed by shallow sulci or, in the smallest specimens, a single sulcus. To this group belong: *B. ornithocephala* (Grev.) R. Ross & P. A. Sims, *B. bonei* R. Ross & P. A. Sims, *B. haitensis* (R. Ross) R. Ross & P. A. Sims, *B. novocastrensis* (R. Ross) R. Ross & P. A. Sims, *B. paratethyos* R. Ross & P. A. Sims, and the imperfectly known *Briggera* sp. I. This last imperfectly known species comes from the Campanian (upper Cretaceous) of the eastern slope of the Ural mountains; thus the earliest record of this group is somewhat later than that for the other group. Although it clearly belongs to the second group rather than the first, this species is in its shape to some extent intermediate between the two. Its sulci are deeper than in any other species of the second group and the outline of its valve is slightly indented opposite them. No other member of this group is known from material of earlier than middle Eocene date, and this gap is a reminder of how incomplete is the fossil record of the diatoms.

The species of this genus have been much confused with one another. This confusion stems primarily from Schmidt's (1889: taf. 142) inclusion under the name *Hemiaulus ornithocephalus* of specimens not only of that species but also of *Briggera includens, B. siberica,* and *B. capitata*. One of us (Ross, 1972) has already discussed this confusion and produced an account of the species then known, except for *B. siberica* and *B. caverna*, not then recognized as belonging with the others. This study was based entirely on observations with the light microscope. Since then some observations made by scanning electron microscopy on species included here in *Briggera* have been published (Ross, Sims & Hasle, 1977). By now, however, specimens of a number of undescribed species have come into our hands and we have made more extensive studies of the previously known species.

Even those authors who were not misled by A. Schmidt into identifying as *Hemialus ornithocephalus* specimens with projections sharply delimited from the central portion of the valve by deep sulci have, for the most part, not recognized the differences between the species of this group but have called all of them *H. includens,* or sometimes, it would seem, *H. sibericus*. As a result the species on which any record of *H. ornithocephalus, H. includens,* or *H. sibericus* is based is uncertain unless it is accompanied by an illustration that shows the diagnostic features of the species or by a reference to one particular figure. It is for this reason that we have not mentioned records under these names in many publications, especially Russian ones.

In the account of the species that follows we deal first with those in which the central portion is sharply delimited from two projections, and follow these with accounts of the species with elliptical to sub-circular valves. Within each group we deal with the species in the order in which they appeared in the fossil record, and the order in which the two groups are dealt with was decided on the same basis. It is for this reason that the type species of the genus is not treated first. We have, however, left to the last the one species of which we have insufficient material to give an adequate description and a name but refer to as *Briggera* sp. I.

Key to the species

1a Valve outline opposite the valve centre concave .... 9. ***caverna*** (p. 309)
1b Valve outline opposite the valve centre convex:
2a Valve crossed by a single sulcus:
3a Height to the top of the marginal ridge at the centre 30 μm or more; no vertical line of areolae on the distal side of the elevation .... 11. ***bonei*** (p. 312)
3b Height to the top of the marginal ridge at the centre 20 μm or less; vertical line of areolae on the distal side of the elevation present. .... 10. ***ornithocephala*** (p. 309)
2b Valve crossed by two or more sulci:
4a Valve with projections sharply distinct from the central portion and separated from it by deep transverse sulci:
5a Marginal ridge surrounding whole valve. .... 5. ***capitata*** (p. 303)
5b Marginal ridge interrupted at the apices:
6a Projections cuneate distally and their width 4/5 or more of the width of the central portion .... 8. ***robusta*** (p. 308)
6b Projections not cuneate distally or their width 3/4 or less of the width of the central portion:
7a Elevations less than 4 μm in diameter. .... 3. ***siberica*** (p. 300)
7b Elevations 4 μm or more in diameter:
8a Projections semicircular to elliptical to clavate in outline, rounded distally:
9a Only one oblique linking spine on each elevation projecting above its summit. 4. ***monoligata*** (p. 302)
9b Two or more erect linking spines projecting above the summit of each elevation:
10a Elevations arising from the apex of the valve without any indentation on the distal side at their base, linking spines extending across the whole width of the elevations .... 1. ***includens*** (p. 294)
10b Elevations arising slightly proximal to the apices of the valve, linking spines occupying only the central part of the elevations. .... 6. ***vemae*** (p. 305)
8b Projections widening little, if any, distal to the sulcus separating them from the central portion of the valve, cuneate distally:
13a Marginal ridge continuous from one elevation to the other. 2. ***morenoensis*** (p. 299)

13b Marginal ridge interrupted opposite the central portion of the valve. 7. ***affixa*** (p. 306)

4b Valve elliptical to subcircular, or subrhombic with the margin very slightly indented opposite the sulci:

14a A vertical row of areolae on the distal face of the elevations:

15a Valve subrhombic with the margin very slightly indented opposite the sulci. ***Briggera* sp. I** (p. 316)

15b Valve elliptic to subcircular, with the margin not indented opposite the sulci:

16a Elevations arising slightly proximal to the apices, their tips swollen distally as much as proximally; marginal ridge opposite the valve centre less than 5 μm deep. 10. ***ornithocephala*** (p. 309)

16b Elevations arising at the apices, their tips much more swollen proximally than distally; marginal ridge opposite the valve centre more than 7·5 μm deep. 14. ***paratethyos*** (p. 315)

14b No vertical row of areolae on the distal face of the elevations:

17a Margin of valve slightly indented opposite the deep sulci .... 5. ***capitata*** (p. 303)

17b Margin of valve not indented opposite the shallow sulci:

18a Elevations with their subglobular tips sessile on the inflated distal parts of the valve 11. ***bonei*** (p. 312)

18b Elevations columnar below their swollen tips:

19a Pseudocelli not divided by a vertical, almost hyaline space 10. ***ornithocephala*** (p. 309)

19b Pseudocelli divided by a vertical, almost hyaline space:

20a Valves 25 μm or more tall at the centre, domed................... 12. ***haitensis*** (p. 313)

20b Valves not more than 15 μm tall at the centre, not domed. 13. ***novocastrensis*** (p. 314)

1. **Briggera includens** (Grunow) R. Ross & P. A. Sims, **comb. nov.** (Pl. 1 figs 1–9)

Hemiaulus includens Grunow in *Denkschr. Akad. Wiss. Wien* **48** (2): 64, t. 2 figs 36–38 (1884); Witt in *Zap. imp. miner. Obshch.* II, **22**: 162, t. 6 fig. 5, t. 9 fig. 6 (1886), excl. syn. Grev.; Jousé in Proshkina-Lavrenko et al., *Diat. Anal.* **2**: 189, t. 73 fig. 1 (1949); R. Ross in *Trans. bot. Soc. Edinb.* **41**: 329, fig. 1 (1972); Strel'nikova, *Diat. Pozdn. Mela* (*Zap. Sibir'*): 101, t. 48 figs 1(?), 2a(?), 3a, 4(?), 6 (1974) excl. t. 48 figs 2b, 3b, 5 et syn. Grev., Grove & Sturt, A. Schmidt quoad t. 142 figs 35, 39 et Jousé quoad t. 72 fig. 14b.

Hemiaulus payeri Grunow, tom. cit.: 64, t. 2 fig. 39 (1884).

Hemiaulus latus A. Schmidt, *Atlas Diat.*: t. 142 fig. 25 (1889); J. D. Möller, *Lichtdrucktaf. herv. schöner vollst. Möller'scher Diat.-Präp*: t. 6 row 2 figs 21, 22, 24, 25, t. 24 row 7 figs 6–11 (1891), *Verz. Lichtdrucktaf. Möll. Diat.-Präp. enth. Arten*: 43, 156 (1892).

Hemiaulus ornithocephalus var., A. Schmidt. op. cit.: t. 142 figs 26–29 (1889).

? *Biddulphia tridentata* sensu A. Schmidt, op. cit.: t. 142 figs 42–43 (1889), non Weisse.

? *Hemiaulus ornithocephalus* sensu Jousé, tom. cit.: 188 (1949) pro parte, quoad t. 72 fig. 14a, non Grev.

Hemiaulus sp., Benda in *Palaeont. Z.* **39**: 176, t. 24 figs 3–4 (1965).

Valve with a central portion separated from two projections by deep sulci not widening below but inclined below towards the centre of the valve, in the longer specimens less prominent sulci across the projections just proximal to the elevations; valves 23–140 μm long, 15–35 μm broad, 8–20 μm tall at the centre; central portion transversely elliptical, domed; projections semicircular to elliptical to clavate with rounded apices, rising little between the sulci and the elevations, outline in girdle view at the apices vertical and without any indentation. Elevations arising at the apices, stout, inflated above proximally but not distally, sometimes only slightly, the upper part sub-triangular to rounded in cross section and as wide as the valve below it; height to the top of the elevations 10–25 μm, diameter along the apical axis 10–16 μm. A flange-like marginal ridge with a concave upper margin between the elevations and the central portion, opposite which it is interrupted. Areolae poroid, with a weakly raised external rim, *c.* 0·3 μm in diameter, either in radial rows on the valve surface except in the sulci with the areolae and rows *c.* 8 in 10 μm, or irregularly scattered and sparser, absent from the mantle except at the apices, where there is a small group of scattered areolae, 7–12 in 10 μm, on the upper part of the mantle and the lower part of the elevations. Sparse scattered rather short superficial spines usually present on the central portion of the valve. Pseudocelli covering the tips of the elevations except on their proximal side, their areolae 12–20(–26) in 10 μm. Linking spines 3–5 on each elevation, concave towards the centre of the valve, not much expanded above, acuminate, *c.* 15 μm long. 1–3 labiate processes near the centre of the valve. Valvocopula *c.* 15 μm deep, with vertical rows of small areolae *c.* 8 in 10 μm.

Upper Cretaceous — upper Turonian–Coniacian. Oceanographer Canyon, Western North Atlantic, 40° 30′ N, 68° 10′ W, 978–1510 m in depth. Dredge sample D25 (personal coll. J. Fenner).

— Senonian. Danzig Bay, Poland (Schulz, 1935).

— Campanian. Exposure XI(14) near Til'tim, basin of the river Synya, Tyumen'sk oblast, U.S.S.R. (BM SEM 2373–2376, 2493–2494).

Core 82 near Ust'-Man'ya, basin of the river Severnaya Sos'va, Tyumen'sk oblast, U.S.S.R. (BM SEM CB15.116–123, CB19.358–362, CB19.697–700, 2308–2317, 3096–3102; Strel'nikova, 1974). Cores 19, 22, same locality (Strel'nikova, 1974).

Paleocene. Anan'ino, Ulyanovsk oblast, U.S.S.R. (BM 33346, coll. Adams F51, G203, G205, G462, G464, G637, J332, J2600; PH coll. Shulze arr. 983, 984, Gen. coll. 12686; Pantocsek, 1889).

Arkhangel'skoye Kuroyedovo, Ulyanovsk oblast, U.S.S.R. (BM coll. Adams L1; Witt, 1886; Schmidt, 1889).

Smol'kovo, Ulyanovsk oblast, U.S.S.R. (BM coll. Adams D957, J2679).

Ulyanovsk (formerly Simbirsk), Ulyanovsk oblast, U.S.S.R. (BM 9396, 9397, 9398, 9400, 35042, 38245, 38246, 43781, 43782, 54788, 60786, 70116, coll. Adams Bess. 28, Bess. 1125, F815, L21, TS10, SEM B16.13, B16.15–19, CB 9.735–743, CB10.979–992, CB16.622–630, 2860–2877; PH coll. Febiger 691; W coll. Grunow 1570d–h syntypes; Grunow, 1884; Schmidt, 1889). ? end cell (BM SEM CB10.950–957).

'Syzran', U.S.S.R. (for this locality see p. 280 above). (BM coll. Adams Bess. 1669, TS 437).

Sverdlovsk oblast, U.S.S.R. (Jousé in Proshkina-Lavrenko et al., 1949*b*).

Eastern slope of the Ural mountains (Krotov & Shibkova, 1961, quoted in Strel'nikova, 1974).

Paleocene–lower Eocene. Barents Sea, 100–500 m depth, between Franz-Josefs Land and Novaya Zembla (Grunow, 1884). (Date uncertain, more probably Paleocene).

Lower Eocene. Isle of Fehmarn, Germany (Benda, 1965).

Prionersk, Kaliningrad oblast, U.S.S.R. (Strel'nikova, Kaplan & Travina, 1978).

Lower–upper Eocene. 'Carlovo', U.S.S.R. (for this locality see p. 281). (BM SEM CB13.896–899, 3590–3604).

The only information that we have about the girdle of this species comes from two specimens both of which consist of a single frustule with its two valves almost in contact with one another and each with their sibling valve attached, together with a valvocopula, but no more of the girdle, attached to the epivalve of the complete frustule. These specimens are both mounted on microscope slides and we have been able to examine them with the light microscope only.

Most authors have assumed that the name *Hemiaulus includens* Grunow was not the name of a new species but a new combination based on *Biddulphia includens* Ehrenberg (1855: 301), a name which was, however, never validly published; it appears as *nomen nudum* in a list of diatoms from Simbirsk (now Ulyanovsk) and Ehrenberg provided neither description nor figure then or later. Also, Grunow, when publishing *Hemiaulus includens,* queried the identity of his species with *Biddulphia includens* Ehrenb.

The most obvious distinguishing feature of this species when seen in girdle view is the vertical end to the valve without any indentation at the base of the elevation. This feature can be made out in valve view by careful differential focusing, but in this view *Briggera includens* is most readily distinguished from *B. monoligata* R. Ross & P. A. Sims and *B. vemae* R. Ross & P. A. Sims, the other species with clavate projections, rounded apices and large elevations, by the disposition of the linking spines and by the size or cross-sectional shape of the elevations. In *B. includens* the linking spines extend across almost the whole width of the elevation (Pl. 1 figs 7, 9), which is sub-triangular to circular in cross section and no more than 16 μm in apical diameter, whereas in *B. monoligata* the single large linking spine occupies only about half the width of the elevation (Pl. 5 figs 4, 5) which is at least 19 μm in apical diameter, and in *B. vemae* the linking spines also occupy only about half the width of the elevation, which is semicircular in cross section (Pl. 7 figs 5, 8). The differences between the smallest specimens of *B. includens* and both

B. siberica (Grunow) R. Ross & P. A. Sims and *B. affixa* (R. Ross) R. Ross & P. A. Sims are discussed under those species.

Briggera includens has been much confused in the past with other species of the genus. Although Grunow (1884) had maintained *Hemiaulus includens* and *H. capitatus* Grev., the basionym of *Briggera capitata* (Grev.) R. Ross & P. A. Sims, as separate species, Witt (1886) treated *H. capitatus* as a probable synonym of *H. includens*, considering that the epithet of the latter dated from Ehrenberg's publication of *Biddulphia includens* as a *nomen nudum*. In the following year Grove & Sturt (1887*a*), in the course of their account of the late upper Eocene deposit from Oamaru, New Zealand, recorded *H. includens* from there, remarking that *H. capitatus* 'seems a similar form, and perhaps identical.' Their collections show that this record is based on *B. capitata,* which is not uncommon in this material; *B. includens* has never been found in it.

Schmidt (1889: taf. 142) confused *Briggera includens* not only with *B. capitata* but also with *B. ornithocephala* (Grev.) R. Ross & P. A. Sims and *B. siberica,* as mentioned above (p. 292). Of the figures on his taf. 142 labelled '*Hemiaulus ornithocephalus* var.' fig. 26, from 'Archangelsk', i.e. Arkhangel'skoye-Kuroyedovo, and figs 27–29 from 'Simbirsk', now Ulyanovsk, are of *B. includens*, fig. 30 from 'Simbirsk' is *B. siberica* and figs 35, 39 from Oamaru are *B. capitata*. In addition, his figs 34, 36, 37 from Oamaru labelled '*Hemiaulus ornithocephalus* Grev.' are *B. ornithocephala*. Also fig. 25 from 'Archangelsk' labelled '*Hemiaulus latus* A.S.' is *B. includens*. Fig. 32 from 'Archangelsk' has much larger areolae than are normal in *B. includens* and may belong to a separate taxon, perhaps distinct at only an infraspecific level, but without adequate specimens we cannot come to a decision on this. On the same plate Schmidt figures two specimens from 'Simbirsk' under the name '*Biddulphia tridentata* Weisse' (figs 42, 43), saying that this species 'ist kein *Hemiaulus*'. Although there is no indication of linking spines on these two drawings, they look in all other respects like *Briggera includens*, and fig. 42 shows two sibling valves with their elevations in close contact. In fossil material of this age sibling valves of *Biddulphia* are normally found in contact only when still surrounded by the girdle of the parent cell. We therefore think it likely that these figures do indeed represent *Briggera includens*, although there can be no complete certainty unless it were possible to locate and examine the specimens. Schmidt's figures differ quite considerably from Weisse's (1855) original rather crude figures of *Biddulphia tridentata*.

Later in the same year Pantocsek (1889), when recording *Hemialus includens* from Anan'ino, Ulyanovsk oblast, U.S.S.R., noted that two of Schmidt's figures (taf. 142, figs 27, 28) of *H. ornithocephalus* var. were of *H. includens*; it is difficult to understand why he did not recognize that figs 26 and 29 were also of this species. At the same time Pantocsek included *H. pulvinatus* Grev. in the synonymy of *H. includens*, but this is quite erroneous. *H. pulvinatus* is a true *Hemiaulus* with large areolae, narrow elevations that taper upward, and linking spines that do not interlock.

Jousé (in Proshkina-Lavrenko et al., 1949*b*: 189, tabl. 73 fig. 1a, b) records *Hemiaulus includens* from the Paleocene of Ulyanovsk and Sverdlovsk oblasts, U.S.S.R., illustrating the species by two figures copied from Grunow (1884). We have seen many specimens of *Briggera includens* from Ulyanovsk oblast and there is no reason to question the accuracy of the record from Sverdlovsk oblast. At the same time Jousé (tom. cit.: 188, tabl. 72 fig. 14a, b) recorded *Hemiaulus ornithocephalus* from the Paleocene of Ulyanovsk oblast, the upper Cretaceous of Danzig Bay and the Miocene of Barbados. The second and third of these records are presumably taken from the publications of Schulz (1935) and Greville (1865*a*) respectively, the former being based on *B. includens* and the latter on *B. ornithocephala*. The record from Ulyanovsk oblast, whether taken from Schmidt (1889) or based on examination of specimens, is undoubtedly based on *B. includens*. Jousé illustrates her account of *H. ornithocephalus* by two figures, one copied from Schmidt (1889: taf. 142, fig. 35, a figure of *B. capitata* from Oamaru, New Zealand), the other original and of a specimen from the Eocene of Kuibyshev oblast, U.S.S.R., a locality for the species that she does not mention in the text. As, however, she reproduces the same figure on a plate the legend of which is headed by a statement that it illustrates the characteristic complex of diatoms from the lower Syzransk strata of the Paleocene of Ulyanovsk oblast (Jousé in Proshkina-Lavrenko et al., 1949*a*: tabl. IIa, fig. 14), there must be some doubt as to the place of origin of this specimen. This figure is a valve view and may well represent *B. includens*, although there is no indication of linking spines on the elevations and the specimen illustrated may thus be a *Biddulphia*.

Jousé (in Proshkina-Lavrenko et al., 1949*b*: 189, tabl. 95 fig. 6) also described and figured a diatom from the Kamyshin stage (late Paleocene) of Penza oblast, U.S.S.R., as *Hemiaulus includens* var. *saratovianus* ('*saratoviana*'), and she lists it (in Proshkina-Lavrenko et al., 1949*a*) amongst the diatoms occurring in material of that age from the river Chasa in that oblast. According to Glezer (in Glezer et al., 1974: 134) this material is of lower Eocene age. Jousé's description is meagre and her figure crude; the figure might, however, represent either a large specimen of *Briggera includens* or one of *B. monoligata*. As we have found a specimen of *B. monoligata* in a sample which very probably comes from that locality or from the exposure of the same strata on the river Davydovka, also in Penza oblast, it seems more likely that that species, rather than *B. includens*, is the basis of *Hemiaulus includens* var. *saratovianus*.

Strel'nikova (1974: tabl. 48 figs 1–6) figures a number of specimens from the Campanian (upper Cretaceous) deposits from the eastern slopes of the northern Ural mountains under the name *Hemiaulus includens*. Of those figures in girdle view, figs 2a, 3a, and 6, look like *Briggera includens*, whilst fig. 4 looks more like *B. siberica* (Grunow) R. Ross & P. A. Sims, the upper part of its elevations being only 2·5 μm in diameter on a specimen that is 29 μm long. Strel'nikova's fig. 1, of a specimen only 12 μm long, might belong to either species but we have seen specimens of neither as small as this. This specimen does appear to have linking spines and is thus probably a *Briggera*. It seems from figs 2a and 4 that the diatoms depicted in them did not have linking spines but it is impossible to be sure from these illustrations; we believe that the object on the proximal side of the right-hand elevation in fig. 4 is a piece of dirt and not a broken linking spine. If this is so, these figures are presumably girdle views of the *Biddulphia* sp. discussed in the next paragraph. All three of Strel'nikova's figures showing specimens in valve view (figs 2b, 3b, 5) have projections less than half as wide as the central portion of the valve, whereas Paleocene specimens of *Briggera includens* and *B. siberica* have projections at least two thirds as wide as the central portion. In the material from the Campanian of the eastern Ural mountains available to us we have found only four relevant specimens. Two consist of a pair of sibling valves joined by interlocking linking spines that are almost indistinguishable from Paleocene specimens of *B. includens*. One of these pairs is 55 μm long, the other (Pl. 1 figs 2, 4, 6, 9) 80 μm long. In these specimens the projections are rather more than two thirds as wide as the central portion of the valve. However, the valves lack superficial spines, a difference that we do not regard as taxonomically significant, particularly as Strel'nikova's fig. 6 shows an otherwise identical specimen with superficial spines. Also, in these two specimens the areolae in the pseudocelli are denser, 24–26 in 10 μm, than in Paleocene specimens, which have 12–20 areolae in 10 μm in their pseudocelli. The structure of the pseudocelli is not resolved in Strel'nikova's fig. 6.

The other two specimens match in outline Strel'nikova's fig. 5; one is 69 μm long, 34 μm broad at the centre, and with projections that have a maximum breadth of 14 μm; the other (Pl. 30 fig. 3) is 111 μm long, 37 μm broad at the centre, and with projections that have a maximum breadth of 15 μm. In both these specimens there are no linking spines on the elevations but instead a small flattened hyaline area in the centre of their summits. One can be almost certain from Strel'nikova's fig. 5 that the diatom illustrated had no linking spines, but it is not possible to see whether it had a small flattened hyaline area in the centre of the summit of its elevations. No detail of the tips of the elevations can be seen in figs 2b or 3b and, as mentioned above, figs 2a and 4 of specimens in girdle view show no definite indication of linking spines. In the light of the evidence available to us, we conclude that *Briggera includens* is a member of the diatom flora of the Campanian of the eastern Urals and that it is illustrated in Strel'nikova's figs 3a and 6, and possibly also in her figs 1 and 2a. Whether the population of this species from the Campanian should be distinguished at an infraspecific level from those occurring in the Paleocene because of the greater density of areolae in the pseudocelli must await examination of further specimens. There are also in this Campanian flora two species of *Biddulphia* closely resembling *Briggera* *includens*; and the smaller specimens of one of them also resemble *Briggera siberica*. This latter species of *Biddulphia* differs from both species of *Briggera* in the absence of linking spines and in the relatively narrower projections. This species is illustrated in Pl. 30 fig. 3 and in Strel'nikova's figs 2b, 3b, 5, and possibly also her figs 2a and 4, but these two, and her fig. 1, may either be of this *Biddulphia* sp. or of *Briggera includens* or *B. siberica*, but the presence of the latter in this flora must remain an open question. The other species of *Biddulphia* (Pl. 30 fig. 4), mentioned above (p. 289) in the discussion of separation valves, was apparently not seen by Strel'nikova.

Strel'nikova (1974: 101) included the very distinct *Hemiaulus capitatus* Grev. (*Briggera capitata* (Grev.) R. Ross & P. A. Sims) in her concept of *H. includens* as well as the *Biddulphia* sp. with narrow projections and possibly also *Briggera siberica*. It is thus scarcely surprising that she said that this is an unusually variable species. There is an appreciable variation in the pattern of the areolae, which may be in regular radial rows or much sparser and irregularly scattered, with some intermediates occurring. *Hemiaulus payeri* Grunow is based on an example of *B. includens* with sparse and irregularly scattered areolae. Another variation is that shorter specimens have their elevations taller in relation to the central portion of the valve than do longer ones. The amount of variation is, however, not nearly as considerable as Strel'nikova's remark suggests.

In a previous paper by one of us (Ross, 1972), this species was cited as coming from Kuznetsk, Penza oblast, U.S.S.R., from a deposit which Glezer (in Glezer et al., 1974: 135) suggests is probably upper Eocene in date. This record is not repeated here. It was based on specimens present on three microscope slides. One of these, BM 32738, a slide prepared by Comber, has been accidentally destroyed in the interval. However, on another slide prepared by Comber from the same material, BM 32739, we found two specimens of *Briggera*. These and the specimen on BM coll. Adams TS693 previously identified as *Hemiaulus includens* are of *B. robusta* R. Ross & P. A. Sims, a different species described below (p. 308) as new. The specimen on BM coll. Adams M89, which has no linking spines and whose areolae are *c.* 0·7 μm in diameter, is, we suggest above (p. 289), *Biddulphia nova-zealandiae* Wise.

Also, we do not now believe that the diatom from Sengilei, Ulyanovsk oblast, U.S.S.R., that we figured under the name *Hemiaulus includens* (Ross, Sims & Hasle, 1977: pl. 1 fig. 3) belongs to this species. We are uncertain of its identity but consider that it may be a small specimen of *B. monoligata* R. Ross & P. A. Sims; we discuss it more fully under that species (p. 303)

Briggera includens has been reported from various localities other than those from which we have seen specimens. Grunow (1884: 64) recorded it as *Hemiaulus payeri* Grunow from material dredged off Franz-Josef Land that is of Paleocene or Eocene age, more probably the former. Since Schulz (1935: 392), when recording *H. ornithocephalus* from the Senonian (upper Cretaceous) of Danzig Bay, remarks that his specimens match taf. 142 fig. 29 in Schmidt (1889) one can accept his record as very probably based on *B. includens*, particularly as the species is known from the upper Cretaceous of the eastern slope of the Ural mountains. Benda's (1965: 176) record of *Hemiaulus* sp. from the upper Ypresian (lower Eocene) of the Isle of Fehmarn in the south-western Baltic is shown by his accompanying figures to be based on *B. includens*. In addition, we have listed in the distribution of the species three records of *H. includens* from the U.S.S.R. that are not supported by illustrations but, because of their location and geological age, are likely to be correct. Jousé (in Proshkina-Lavrenko et al., 1949*b*) records it from the Paleocene of Sverdlovsk oblast in the U.S.S.R. as well as of Ulyanovsk oblast, from where we have seen specimens. It is also recorded from the Paleocene of the eastern slopes of the Ural mountains in a paper by Krotov & Shibkova (1961) that we have not been able to see but which is quoted by Strel'nikova (1974). In addition, Strel'nikova, Kaplan and Travina (1978) record it from the lower Eocene from Prionersk, near Svetlogorsk, Kaliningrad oblast, U.S.S.R. On the other hand, because of our uncertainties about the identity of *Hemialus includens* var. *saratovianus* from the uppermost Paleocene of Penza oblast, U.S.S.R., and of the specimen from the Eocene of Kuibyshev oblast, U.S.S.R., that Jousé figures (in Proshkina-Lavrenko et al., 1949*b*: tabl. 72 fig. 14a) under the name *H. ornithocephalus*, the locality from which this came also being doubtful, we have not included these records in the distribution of the species.

It should also be mentioned that there is a microscope slide in BM (coll. Adams TS228) mounted by Truan and labelled 'Hungria' that has on it three specimens of *Briggera includens*. It does, however, also contain specimens of a number of other species known from Paleocene deposits of the central Volga basin but not from Hungary. We therefore conclude that the locality is incorrect and that many, although not necessarily all, of the specimens mounted by Truan on this selected slide are from the Paleocene of the central Volga basin, of which he had material, and not from Hungary, the specimen of *B. includens* among them.

Also, Möller (1891: taf. 6 row 3 figs 21, 22, 24, 25) illustrated four specimens that are clearly *Briggera includens* under the name *Hemiaulus latus* A. Schmidt, but stated that they came from Oamaru (Möller, 1892: 43). As no other specimens of this species having been found from Oamaru, all the other records of it from there having been based on misidentifications, we assume that this locality is in error. There are no specimens of *B. includens* on Möller's plate (1891: taf. 26) devoted entirely to specimens from Oamaru, but he does figure six specimens of *B. includens* in his plate of diatoms from Simbirsk (now Ulyanovsk) (Möller, 1891: taf. 24 row 7 figs 6–11) and identifies these as *Hemiaulus latus* (Möller 1892: 156).

One can thus summarize the known distribution of this species in time and space as occurring from the upper Turonian or Coniacian to the lower Eocene in the northern Atlantic and the epicontinental seas around Europe, which at that stage was not united to Asia; the northern Atlantic also was much narrower then. Whether its occurrence in the material from 'Carlovo' means that it persisted until later in the Eocene is an open question (see p. 281 above).

2. **Briggera morenoensis** R. Ross & P. A. Sims, **sp. nov.** (Pl. 2 figs 1–9, Pl. 31 fig. 1)

Frustulum, ubi maturum vel dividens, axe pervalvari longiore quam apicali, 80 μm longo in frustulo perfecto solo viso. Valva portione centrali a projecturis duabus separata sulcis profundis infra non dilatatis sed centrum valvae versus inclinatis; 35–85 μm longa, 17–30 μm lata, ad centrum 15–21 μm alta; portio centralis transverse elliptica, tholiformis; projecturae cuneatae apicibus obtusis, haud alte elevatae, latitudine non majore quam 3/4 latitudinis portionis centralis. Elevationes apicibus parum proximaliter exorientes, extrorsus inclinatae, summis tumidis sphaericis et tam latis quam valva infra eis; altitudo ad vertices elevationum 18–25 μm. Costa marginalis tenuis ab elevatione altera ad alteram in utroque margine valvae, centro valvae opposita non interrupta, sulcis opposita non concava. Areolae poroides, extrinsecus margine elevato, diametro *c.* 0·3 μm, per superficiem valvae, praeter in sulcis, inordinate dispersae, 4–7 in 10 μm, in limbo solum in parte superiore, ubi sparsae, praeter ad apices valvae ubi paucae sed crebriores, 6–8 in 10 μm. Spinae superficiales dispersae in portione centrali et in parte proximali elevationum. Pseudocelli summum tumidum, praeter latus proximalis, utraeque elevationis tegentes, areolis 20–30 in 10 μm. Spinae ligantes in utraque elevatione 3–5, ad partem centralem lateris proximalis verticis limitatae, centrum valvae versus valde concavae, supra parum expansae, *c.* 15 μm longae. 1 vel 2 rimoportulae prope centrum valvae. Cingulum maturum ex 4 minimum taeniis constans; valvocopula 11–12·5 μm profunda, copulae aliae 10–11 μm profunda, pleura 8 μm minimum profunda; copulae apertae, ligulis ad polos alternos positis; secus marginem abvalvarem copularum area hyalina angusta, alibi areolis in seriebus verticalibus 14–18 in 10 μm, areolis 6–20 in 10 μm; pleura areolis et seriebus crebrioribus quam in copulis, seriebus 18–24 in 10 μm, areolis 15–20 in 10 μm.

TYPUS: BM 81100, ex stratis cretaceis ad 'Moreno Gulch, Fresno County, California, U.S.A.

Frustule, when mature or dividing, with the pervalvar axis exceeding the apical axis, 80 μm long in the one complete frustule seen. Valve with a central portion separated from two projections by deep sulci not widening below but inclined below towards the centre of the valve; valves 35–85 μm long, 17–30 μm broad, 15–21 μm tall at the centre; central portion transversely elliptical, highly domed; projections cuneate with obtuse apices, not highly raised, their width not exceeding 3/4 that of the central portion. Elevations arising somewhat proximal to the apices, inclined outwards, their swollen tips spherical and as wide as the valve below them; height to the tops of the elevations 18–25 μm. A flange-like marginal ridge running from one elevation to the other on either side of the valve, not interrupted opposite the centre of the valve, its free edge not concave opposite the sulci. Areolae poroid, with a raised rim on the outer surface of the valve, *c.* 0·3 μm in diameter, irregularly scattered over the valve surface but absent in the sulci, 4–7 in 10 μm, on the mantle present only on the upper part and there sparse except at the apices, where there is a small group of areolae 6–8 in 10 μm. Scattered superficial spines present on the central portion of the valve and on the proximal part of the elevations.

Pseudocelli covering the swollen tips of the elevations except for their proximal sides, their areolae 20–30 in 10 μm. Linking spines 3–5 on each elevation, on the central part only of the proximal side of the summit of the elevation, strongly concave towards the centre of the valve, not much expanded above, *c.* 15 μm long. 1 or 2 labiate processes near the centre of the valve. Mature cingulum of at least four elements, the valvocopula 11–12·5 μm deep, the other copulae 10–11 μm deep, and distal to this a pleura at least 8 μm deep; copulae open bands, the ligulae at alternate poles; copulae with a narrow hyaline area along the abvalvar margin, elsewhere with areolae in vertical rows, rows 14–18 in 10 μm, areolae 6–20 in 10 μm, closer on the abvalvar part of the band than on the advalvar; pleura with areolae and rows closer, rows 18–24 in 10 μm, areolae 15–20 in 10 μm.

Upper Cretaceous — Maastrichtian. Moreno shale, Moreno Gulch, Fresno county, California, U.S.A. (BM81100, 81101, SEM, B17.771–779, CB14.183–199, CB14.716–724, CB14.729–732, CB16.684–700, CB17.062–067, 2013–2057, 3971–3978).

The information about the girdle available for this species is more detailed than it is for many, but even so it is not possible to give a complete and unequivocal description. Only two specimens approximating to complete frustules were seen by us and both of these were somewhat damaged. One of these is illustrated as Pl. 2 fig. 2.

The species that most closely resemble *Briggera morenoensis* are *B. affixa* (R. Ross) R. Ross & P. A. Sims and *B. robusta* R. Ross & P. A. Sims. Both these two come from much later deposits, upper Eocene as against the upper Cretaceous age of *B. morenoensis*. All three are similar in outline, but in *B. affixa* the projections are narrower relative to the central portion of the valve than in *B. morenoensis*, whilst in *B. robusta* they are wider. In *B. affixa* and *B. robusta* the valve surface is raised much higher immediately proximal to the base of the elevation than it is in *B. morenoensis*. Another point of difference between *B. morenoensis* and *B. affixa* is the fact that in the former the marginal ridge is continuous from one elevation to the other (Pl. 2 fig. 5), whereas in the latter is does not cross the central portion of the valve (Pl. 8 fig. 1).

This species has been found only in the Moreno Shale from California, a deposit laid down during the Maastrichtian stage of the upper Cretaceous. Although there have been a number of papers dealing with the diatom flora of this deposit, its presence there is not recorded in any of them. Our current knowledge of the upper Cretaceous diatom floras of the world is so scanty that we cannot tell whether its restricted distribution in both space and time is apparent or real.

3. **Briggera siberica** (Grunow) R. Ross & P. A. Sims, **comb. nov.** (Pl. 3 figs 1–7)

Hemiaulus sibericus Grunow in *Denkschr. Akad. Wiss. Wien* **48** (2): 64, t. 2 figs 34, 35 (1884); A. Schmidt, *Atlas Diat.*: t. 118, fig. 8 (1888); Jousé in Proshkina-Lavrenko et al., *Diat. Anal.* **2**: 187, t. 72 fig. 6 (1949).

Hemiaulus ornithocephalus var., A. Schmidt, op. cit.: t. 142 fig. 30 (1889).

Hemiaulus sp., A. Schmidt, op. cit.: t. 142 figs 31, 44, 45 (1889).

Hemiaulus latus sensu J. D. Möller, *Lichdrucktaf. herv. schöner vollst. Möller'schen Diat.-Präp*: taf. 24 row 7 fig. 12 (1891), *Verz. Lichtdrucktaf. Möll. Diat.-Präp. enth. Arten*: 156 (1892), non A. Schmidt.

Valve with a central portion separated from two projections by deep sulci not widening below but inclined below towards the centre of the valve, 19–70 μm long, 12·5–17 μm broad, 11–15 μm tall at the centre; central portion transversely elliptical, domed; projections cuneate with obtuse apices to clavate, except in the smallest specimens raised very little distal to the sulcus separating them from the central portion, then crossed by another sulcus distal to which they rise more strongly to the base of the elevations, the smallest specimens with projections rising directly to the base of the elevations from the sulci separating them from the central portion of the valve. Elevations columnar, arising at or just proximal to the elevations, 2–3·5 μm in diameter, very slightly or not at all inflated above; height to the top of the elevations 15–20 μm. A flange-like marginal ridge between the elevations and the central dome, its free edge moderately to strongly concave. Areolae poroid, with a weakly raised external rim, *c.* 0·3 μm in diameter, in radial rows on the valve surface but absent in the sulci, areolae *c.* 18 in 10 μm, rows *c.* 14 in 10 μm, absent on the mantle except on the upper part at the apices, where there is a small group. Very short superficial spines usually frequent on the central portion of the valve and sparse on the projections, sometimes absent. Pseudocelli small, on the distal part of the upper half of the tips of the elevations, their areolae 25–30 in 10 μm. A very small linking spine, perhaps more than one, on the proximal edge of the summit of the elevations. 1 or 2 labiate processes near the centre of the valve, their external tubes *c.* 3 μm long.

Paleocene. Anan'ino, Ulyanovsk oblast, U.S.S.R. (BM coll. Adams G462, G464).

Ulyanovsk (formerly Simbirsk), Ulyanovsk oblast, U.S.S.R. (BM SEM CB10.958–960, CB16.618–621, 2878–2883, 3761–3771; W coll. Grunow 1570d – h-syntypes; Grunow, 1884; A. Schmidt, 1888, 1889).

'Syzran', U.S.S.R. (for this locality see p. 280 above) (BM 32624, coll. Adams TS437).

?Sverdlovsk oblast, U.S.S.R. (Jousé in Proshkina-Lavrenko et al., 1949*b*).

We have seen only single valves of this species and can say nothing of its girdle. The specimens that we have been able to examine with the scanning electron microscope have broken linking spines and we have not been able to distinguish any detail of these structures on the specimens that we have examined with the light microscope; we can accordingly not be certain that this species has interlocking linking spines. We have decided, however, to transfer it to *Briggera* in spite of this uncertainty because it has all the other characters of the genus and it is clearly not a *Hemiaulus*.

The smallest specimens of *Briggera includens* and *B. affixa* might be confused with this species. Those of *B. includens* can have elevations no more than 4 μm in diameter, although they are usually much stouter. However, *B. siberica* can be distinguished from *B. includens* because the latter has much larger linking spines and more distant areolae both on the valve and in the pseudocelli. Again, although the smallest specimens of *B. affixa* can have a similar outline, they too have stouter elevations and they have a much larger group of areolae at the apices on the upper part of the mantle and the lower part of the elevations.

Four of the figures on taf. 142 of Schmidt (1889) illustrate this species. All are of specimens from 'Simbirsk', now Ulyanovsk; one, fig. 30, is labelled '*Hemiaulus ornithocephalus* var.', as also are figures of *Briggera includens* and *B. capitata* on the same plate; the identity of the other three, fig. 31, 44, 45, is given as 'fräglich'.

The only specimens of this species that we have seen or of which we have seen illustrations come from the Paleocene of the central Volga basin (Ulyanovsk and perhaps Kuibyshev oblasts). However, Jousé (in Proshkina-Lavrenko et al., 1949*b*) records it as *Hemiaulus sibericus* from the Paleocene of Sverdlovsk oblast as well as Ulyanovsk oblast. As her figures of the species (op. cit.: tabl. 72 fig. 6a, b) are both copied from Grunow (1884) there can be no complete certainty as to the identity of the diatom on which her record from Sverdlovsk oblast is based, although it may be correct as her description agrees well with this species. However, she (Jousé, 1955) later records *Hemiaulus sibericus* as coming from the lower Eocene of the eastern slopes of the Ural mountains and western Siberia, but accompanies these records with an illustration (Jousé, 1955: tabl. 2 fig. 9) of a species of *Hemiaulus* sensu stricto. There is thus considerable doubt about the age and identity of the specimens on which she based her 1949 record from Sverdlovsk oblast. Paramonova (1964) records *Hemiaulus sibericus* from the lower Eocene up to the transition to the lower Oligocene in deposits from the north-eastern part of the basin of the river Ob (north-western Siberia). However, amongst material that we received from Mr Brigger is a sample labelled 'N. Siberia, River Ob, late Eocene'. This we presume to be from one of the deposits studied by Paramonova. We have seen no specimens of *Briggera siberica* in this material, but it does contain *B. affixa*. As we point out above, this is a species that has considerable similarites with *B. siberica* and it is thus possible that Paramonova's records are based, at least in part, on *B. affixa*. It is however even more likely that her records are based on specimens of *Hemiaulus* matching Jousé's (1955) illustration discussed earlier in this paragraph. Also, as we mentioned above (p. 297) when discussing Strel'nikova's record of *Hemiaulus includens* from the Campanian (upper Cretaceous) of the eastern slopes of the northern Ural mountains, there is a possibility that *B. siberica* occurs there.

4. **Briggera monoligata** R. Ross & P. A. Sims, **sp. nov.** (Pl. 4 figs 1–6, Pl. 5 figs 1–7, Pl. 31 fig. 2)

?*Hemiaulus includens* var. *saratovianus* Jousé in Proshkina-Lavrenko et al., *Diat. Anal.* **2**: 189, tabl. 95 fig. 6 (1949).

?*Hemiaulus includens* sensu R. Ross, P. A. Sims & Hasle in *Beih. nov. Hedwigia* **54**: 181, t. 1 fig. 3 (1977), non Grunow.

Frustulum, ubi maturum, axe pervalvari axem apicalem aequanti vel excedenti. Valva portione centrali a projecturis duabus separata sulcis profundis infra non dilatatis; 60–135 μm longa, 24–28 μm lata, ad centrum 22–27 μm alta; portio centralis circularis, tholiformis; projecturae clavatae, apicibus rotundatis, latitudine maxima 5/6 ejus portionis centralis, haud alte elevatae, utraque sulco altero ad basim elevationis traversa. Elevationes ad apices valvae exorientes, aspectu valvari circulares vel sub-triangulares, summis tam latis quam valva infra eis, sed plerumque infra summis parum constrictae, vix altiores quam portio centralis, verticibus complanatis; altitudo ad vertices elevationum 23–30 μm, diameter in axe apicali 19–35 μm. Costa marginalis tenuis inter elevationes et portionem centralem, plerumque trans portionem centralem porcae parvae ad instar continua. Areolae poroides, extrinsecus margine elevato, diametro 0·2–0·8 μm, in superficie valvae inordinate dispersae, 2–5 in 10 μm, in limbo ad apices et plerumque portioni centrali oppositae praesentes, in partibus inferioribus constrictis elevationum plerumque carentes. Spinae superficiales dispersae, *c.* 2 in 10 μm, in portione centrali. Pseudocelli in partibus elevationum distalibus et lateralibus supra constrictionem, areolis suis in seriebus ex centro suo radiatis, seriebus et areolis 10–12 in 10 μm. Spinae ligantes in utraque elevatione 2, altera 10–12 μm alta, centrum valvae versus vix concava, versus et trans axem apicalem oblique inclinata, altera parva, supra verticem elevationis non exstans. Rimoportulae 2, una prope marginem utramque centro opposita. Utrumque cingulum frustuli maturi ex 5 minimum taeniis constans, utraque, praeter valvocopulam, ligula forti instructa; pars exterior valvocopulae *c.* 10 μm profunda, pleurarum 12–5 μm profunda, pleura maxime abvalvari minime profunda; valvocopula areolis dispersis 3–8 in 10 μm, pleurae areolis in seriebus verticalibus dispositis, seriebus 15–18 in in 10 μm, areolis 10–15 in 10 μm.

TYPUS: BM 81102, ex stratis eocaenicis ad 'Singiliewsky', ut videtur 'Sengilei, Ulyanovsk oblast, U.S.S.R.'

Mature frustules with the pervalvar axis equalling or exceeding the apical axis. Valve with a central portion separated from two projections by deep sulci not widening below; 60–135 μm long, 24–28 μm broad, 22–27 μm tall at the centre; central portion circular, domed; projections clavate with rounded apices, their greatest width 5/6 of to equal to that of the central portion, their surface not much raised distal to the sulci separating them from the central portion, crossed by a second shallow sulcus at the base of the elevations. Elevations arising at the apex of the valve, circular to sub-triangular in cross section, their tips as wide as the valve below them, but a slight constriction present usually all around below the tips, very little taller than the central portion of the valve and with flattened summits; height to the summits of the elevations 23–30 μm, diameter along the apical axis 19–35 μm. A flange-like marginal ridge between the elevations and the central portion of the valve, usually continued across the central portion as a slight ridge. Areolae poroid, with a raised external rim, 0·2–0·8 μm in diameter, irregularly scattered over the valve surface, 2–5 in 10 μm, present on the mantle at the apices and usually opposite the central portion of the valve, usually absent from the constricted lower part of the elevations. Central portion of the valve with scattered superficial spines, *c.* 2 in 10 μm. Pseudocelli covering the distal and lateral sides of the elevations above the constriction, their areolae in rows radiating from their centre, rows and areolae 10–12 in 10 μm. Linking spines 2 on each elevation, one of them 10–12 μm tall, scarcely concave towards the centre of the valve, inclined obliquely towards and across the apical axis, the other small and not projecting above the summit of the elevation. Labiate processes 2, near the margin on each side of the valve opposite the centre. Each cingulum of a mature frustule consisting of at least 5 open bands, each, except the valvocopula, with a well developed ligula, the valvocopula with a pars exterior *c.* 10 μm deep, the pars exterior of the pleurae 12–5 μm deep, the most abvalvar the least deep; valvocopula with scattered areolae 3–8 in 10 μm, the pleurae with areolae in vertical rows, rows 15–18 in 10 μm, areolae 10–15 in 10 μm.

Lower Eocene. 'Singiliewsky' (presumed to be Sengilei, Ulyanovsk oblast, U.S.S.R.) (BM 81102, SEM CB20.402–411, 3380–3407, 3413–3433, 3543–3583, 3586–3589).

Penza oblast, U.S.S.R. (for this locality see p. 281 above) (BM SEM 3176–3201).

One specimen of this species (Pl. 4 figs 5, 6) consisted of a pair of sibling valves surrounded by the somewhat broken remains of the girdle of the parent frustule, and it is from this specimen that the description of the girdle has been drawn up. The other specimens had no girdle elements attached.

The character of the linking spines, of which there is only one of each elevation that projects above its summit, is the basis of our choice of epithet for this species. This arrangement of the linking spines is unique within the genus. The single large linking spines on the two contiguous elevations of a pair of sibling valves hold these together because they are each inclined towards and across the apical axis of the valve with the result that the tip of one lies behind the base of the other; lateral movement is prevented on one side by the small flange-like linking spine on the other side of the apical axis to the large spine, and on the other by a raised part of the base of the large linking spine (Pl. 4 figs 2–4).

Apart from this considerable difference in the linking spines, *Briggera monoligata* resembles *B. includens* very closely. Its valve has a similar outline, its projections are little raised between the central portion of the valve and the elevations (Pl. 5 fig. 2), and the areolae of the pseudocelli are as widely spaced as in *B. includens* (Pl. 4 figs 2, 4; Pl. 5 fig. 6); in all other species of the genus they are much closer. There are, however, other differences than those of the linking spines between the two species. In *B. monoligata* the elevations are usually slightly constricted below their tips distally and laterally as well as proximally (Pl. 4 fig. 1; Pl. 5 fig. 2) and they are larger than in *B. includens*; also in *B. monoligata* there is less difference in height between the elevations and the central portion of the valve, with the result that sibling valves are almost in contact at their centres (Pl. 4 fig. 1). Nevertheless, the close resemblance in most respects between the two species, together with their occurrence in the same geographical area, suggests strongly that there is an evolutionary connection between them, with *B. includens*, which occurs earlier in the fossil record, possibly an ancestor of *B. monoligata*.

As we point out (p. 297) the most probable basis of *Hemiaulus includens* var. *saratovianus* Jousé is a specimen of *Briggera monoligata*. Jousé (in Proshkina-Lavrenko et al., 1949*a*: 127) recorded the variety from Kamyshin strata exposed on the river Chasa in Penza oblast, and we believe that specimens received from Mr Brigger and labelled 'Penza, lower Eocene' came from this outcrop or from the same strata exposed on the river Davydovka, also in Penza oblast. Amongst these specimens labelled 'Penza, lower Eocene' was an example of *B. monoligata*.

There is a specimen (BM SEM B.429–437, CB.17.068–070) consisting of a single valve from the material labelled 'Singiliewsky' that we previously identified as *Hemiaulus includens* (Ross, Sims & Hasle, 1977: 181–182, pl. 1 fig. 3) but now consider does not belong to that species. This specimen has elevations that are slightly constricted all around below their tips and it also apparently had linking spines with the same arrangements as those of *Briggera monoligata*. On the proximal side of the summit of each elevation it has a single somewhat oblique groove with an intact flange on one side and the broken base of a linking spine on the other. This specimen, however, is much smaller than those on which the description of *B. monoligata* is based and it differs from them in various other ways. It is 28 μm long, 17·5 μm broad, 14 μm tall at the centre and the height to the summit of its elevations is 24 μm. The tips of the elevations are much more rounded above than those of *B. monoligata* and also much smaller, being only 6 μm in diameter, the areolae of the pseudocelli are much denser, 25–30 in 10 μm, and there is a single labiate process in the centre of the valve. In other species of *Briggera* of which we have seen a continuous range of specimens over a wide range of apical length, the smallest differ in shape from the largest in much the same way as this one differs from those on which we have based our description of *B. monoligata*. In this case, however, the other differences are greater than they are in those species of which we have seen a continuous range and, in the absence of intermediates, we hesitate to identify this specimen as *B. monoligata*, although considering it very probable that it belongs there.

5. **Briggera capitata** (Grev.) R. Ross & P. A. Sims, **comb. nov.** (Pl. 6 figs 1–9)

Hemiaulus capitatus Grev. in *Trans. microsc. Soc. Lond.* II, **13**: 54, pl. 6 fig. 24 (1865); R. Ross in *Trans. bot. Soc. Edinb.* **41**: 333, fig. 3 (1972).

Hemiaulus includens sensu Grove & Sturt in *J. Quekett microsc. Cl.* II, **3**: 11 (1887), non Grunow; J. D. Möller, *Lichtdrucktaf, herv. schöner vollst. Möller'scher Diat.-Präp.*: t. 6 row 2 figs 1–3, t. 26 row 6 figs 14–15, 20–21 (1891), *Verz. Lichtdrucktaf. Möll. Diat.-Präp enth. Arten*: 42, 165 (1892); Wise in *Ann. Mag. nat. Hist.* XII, **5**: 404, pl. 20 fig. 1 (1952).

Hemiaulus ornithocephalus var., A. Schmidt, *Atlas Diat.*: t. 142 fig. 35, 39 (1889);? Fenner in *Init. Rep. Deep Sea Drilling Proj.* **39**: 521, t. 31 figs 13, 14 (1977).

Hemiaulus payeri sensu J. D. Möller, *Lichtdrucktaf. herv. schöner vollst. Möller'scher Diat.-Präp.*: t. 26 row 6 fig. 22 (1891), *Verz. Lichtdrucktaf. Möll. Diat.-Präp. enth. Arten*: 165 (1892), non Grunow.

Hemiaulus ornithocephalus sensu Jousé in Proshkina-Lavrenko et al., *Diat. Anal.* **2**: 188 (1949) pro parte, quoad t. 72 fig. 14b, non Grev.

Frustules with the pervalvar axis up to five times as long as the apical axis. Valve with a central portion separated from two projections by deep sulci widening below, the smallest specimens sub-elliptical; valves 20–180 μm long, 14–70 μm broad, 20–40 μm tall at the centre; central portion transversely elliptical, highly domed, but the dome much reduced in the smallest specimens; projections widening distal to the sulci very slightly or not at all, semicircular in outline or sub-cuneate with rounded apices. Elevations arising slightly proximal to the apices, almost as large as the projections, their swollen tips spherical and as wide as the valve below them; height to the top of the elevations 35–65 μm. A flange-like marginal ridge surrounding the whole valve with its upper edge almost as high as the top of the central portion of the valve, or much higher than it in the smallest specimens where the central dome is reduced. Areolae poroid, with a weakly raised external rim, 0·7–1·5 μm in diameter, irregularly scattered or in radial rows on the valve surface, areolae and rows 5–7 in 10 μm, absent in the troughs of the sulci, on the elevations except close to the pseudocellus, and on the mantle except in the apical region. No superficial spines (except on one specimen of doubtful identity). Pseudocelli covering the distal half of the swollen tips of the elevations, areolae 15–22 in 10 μm. Linking spines 3–4 on each elevation, arising from the middle part only of the proximal edge of the summit of the elevation, much widened above, acute, not very concave towards the valve centre, about 10 μm long. No labiate process seen. Valvocopula an open band *c.* 20 μm deep, next girdle band *c.* 16 μm deep and with a ligula, both with areolae irregularly spaced in vertical rows, areolae 3–7 in 10 μm, rows 8–10 in 10 μm, and on the second band a single horizontal row of areolae *c.* 14 in 10 μm near the advalvar edge of the pars exterior.

Middle Eocene. Cambridge Estate, Barbados (BM 3426 holotype; Greville, 1865*b*).

[South-western edge of the São Paulo plateau, South Atlantic, 28° 17.22′ S, 41° 05.28′ W, 3203 m depth. Deep Sea Drilling Project core 356 (Fenner, 1977). An uncertain record, see p. 305.]

Upper Eocene. Oamaru, Otago Province, New Zealand (BM9392, 11241 (Jackson's Paddock), 11248 (Jackson's Paddock), 30816 (Jackson's Paddock), 30817 (Jackson's Paddock), 30819 (Jackson's Paddock), 30848, 30849, 31341, 31548, 32809 (Jackson's Paddock), 32810 (Jackson's Paddock), 32816, 32820, 33204, 33206, 33313 (Jackson's Paddock), 33317 (Jackson's Paddock), 35032 (Dick's Farm), 35033 (Dick's Farm), 35374 (Dick's Farm), 35375 (Dick's Farm), 35479 (Cormack's Siding), 35688 (Allan's Farm), 35914 (Papakaiyo, lower), 36097 (Forrester's Hill), 36299 (Allan's Farm), 38249 (Forrester's Hill), 38250, 43783, 46553, 46555, 46575, 46597, 52755, 55275 (Jackson's Paddock), 60776 (William's Bluff), 60778 (Borries), 60780 (Jackson's Paddock), 60781, 60783, 60784, 60785, 61344 (Jackson's Well), 61354 (Jackson's Well), 64041, 70117, 73746, 74051, 74054, 74056 (Papakaiyo), 74057 (Papakaiyo), 75121, 76321, 76322, 77142 (Cave Valley), coll. Adams B228, Bess. 327, G132 (Troublesome Gulley), G187, G600, G619, G659 (Troublesome Gulley), GC644, GC1141, GC1615, GC1616 (Totara), GC1618, GC1619, GC2792, J330, J331, J958 (Jackson's Paddock), J4178, L35 (Allan's Farm), TS23, TS270, TS271, TS272 (Jackson's Paddock), TS289, TS292, TS949 (Bain's Farm, lower), SEM B11.481 (Allan's Farm), B11.483–484 (Allan's Farm), B11.486 (Allan's Farm), B15.67–74, CB01.105–108 (Allan's Farm), CB01.117 (Allan's Farm), CB10.126–134, CB16.566–576, CB16.809–823, CB16.825, CB17.577–580, CB17.582–584, CB17.586–587, 2069–2110, 4715–4730, 4804–4806; PH coll. Shulze arr. 57, 59, 1563, coll. Boyer H-1-2, Gen. coll. 20087, 89095, 89163 (Jackson's Paddock); Grove & Sturt, 1887*a*; A. Schmidt, 1889; Wise, 1952).

The information about the girdle in the description of the species comes from one specimen only; this has two girdle bands attached to one valve and this is probably not the complete cingulum.

The type specimen of this species has no linking spines. It comes from the late middle Eocene of Cambridge, Barbados, and no other specimen of the species from the fossil deposits on that island has been reported. It is, however, completely identical with specimens found rarely in the late upper Eocene of Oamaru, New Zealand, along with which there occur much more frequent specimens differing only in the presence of interlocking linking spines. We accordingly consider both the Oamaru specimens without linking spines and the single specimen from Cambridge, Barbados, as end valves of colonies, a view already expressed by one of us (Ross, 1972). Some doubt must, however, remain as to whether the name *Briggera capitata* is correctly applied to this species.

As indicated in the synonymy above, this species has been confused with both *Briggera includens* and *B. ornithocephala*, from both of which it is clearly distinct. Authors other than those cited in the synonymy of this species, e.g. Strel'nikova (1974), have included references to it in their synonymy of one or other of these two species, for which they have, of course, used the basionyms *Hemiaulus includens* and *H. ornithocephalus*, These confusions are discussed at length under *B. includens* (p. 296).

Most of the other species of *Briggera* that resemble *B. capitata* in having projections separated from the central portion of the valve by deep sulci differ from it in having elevations that are not so tall and do not exceed the central portion of the valve in height by nearly so much. Only *B. affixa* and *B. vemae* can have elevations as tall as those of *B. capitata*. In *B. affixa* superficial spines are normally present, the areolae are smaller, those of the pseudocelli are more closely spaced, and the elevations are not so stout. *B. vemae* has each of its projections crossed by a second sulcus just proximal to the elevations, it has superficial spines and its areolae are smaller.

In this species, but apparently in none of the others with deep sulci, the smallest valves are sub-elliptical in outline with the projections not sharply distinct from the central portion, although there is a slight indentation opposite the sulci. Even the smallest have two sulci and a small dome between them; one such was illustrated by Ross (1972: fig. 3B) and another is shown as Pl. 6 fig. 5.

Fenner (1977: 521, pl. 3 figs 13, 14) recorded *Hemiaulus ornithocephalus* var. from the middle Eocene of a core recovered from the south-western edge of the São Paulo plateau off the Brazilian coast. Even although the figures from Schmidt (1889: taf. 142 figs 26–29) that she cites represent *Briggera includens* her own figures suggest that the diatom she found there is more probably *B. capitata*. The size of its areolae and their distance apart match *B. capitata* rather than *B. includens*, as do the shape of its projections and the breadth of the valve relative to its length. On the other hand, her specimen has superficial spines on the central portion and these are present on none of the specimens certainly belonging to *B. capitata*. However, in other species of *Briggera* the presence or absence of superficial spines does not seem to be a character of appreciable taxonomic importance. From Fenner's figures one cannot see whether the marginal ridge extends around the whole valve or was only present between the elevations and the central portion of the valve, neither can one tell how much higher than the central portion of the valve the elevations reach nor how much of the proximal edge of their summits is occupied by linking spines; these are the characters by which the species can be distinguished with some certainty. We believe from its morphology that this specimen is more likely to be *B. capitata* than *B. includens* and this is more consistent with its age and location. We have therefore included it here with a query.

One can say of this species with certainty, therefore, that it is comparatively common in the late Eocene of Oamaru, New Zealand; with less confidence one can add that it occurs in the late middle Eocene of Barbados and perhaps also in the middle Eocene from off the coast of Brazil.

6. **Briggera vemae** R. Ross & P. A. Sims, **sp. nov.** (Pl. 7 figs 1–9, Pl. 31 fig. 3)

Valve portione centrali a projecturis duabus separata sulcis profundis infra non dilatatis, 140–170 μm longa, 32–40 μm lata, ad centrum 20–30 μm alta; portio centralis late elliptica, tholiformis; projecturae clavatae apicibus rotundatis, latitudine maxima eam portionis centralis aequanti et ad marginem proximalem elevationis, parte proximali tholiformi, tam alta quam portio centralis, distali sulco lato et non profundo elevatione tenus. Elevationes apicibus parum proximaliter insertae, parte sub summo tumido vix facta, summo tumido aspectu valvari semicirculari et tam lato quam valva; altitudo ad verticem elevationum 30–40 μm. Costa marginalis tenuis ab elevatione altera ad alteram in utroque margine valvae. Areolae poroides, extrinsecus margine leniter elevato, diametro *c.* 0·5 μm, in superficie valvae in seriebus radialibus interruptis dispositae, areolis 12–15 in 10 μm, seriebus *c.* 13 in 10 μm, in sulcis proximalibus carentes, in limbo solum in parte superiore ad apices et portione centrali partibusque tholiformibus projecturarum oppositae. Spinae superficiales longae validaeque in portione centrali valvae et in partibus tholiformibus projecturarum dispersae. Pseudocelli dimidium distale summorum elevationum tegentes, areolis in seriebus quae in lineam centralem valvae ad angulum conveniunt, areolis et seriebus *c.* 22 in 10 μm. Spinae ligantes in utraque elevatione 3–4, ad partem centralem lateris proximalis verticis elevationis limitatae, centrum valvae versus concavae, ad apices acuminatae, *c.* 15 μm longae. Rimoportulae 4–5, prope centrum valvae.

TYPUS: BM 81103, ex stratis eocaenicis de profundis maris Atlantici australis.

Valves with a central portion separated from two projections by deep sulci not widening below, 140–170 μm long, 32–40 μm broad, 20–30 μm tall at the centre; central portion broadly elliptical, domed; projections clavate with rounded apices, their greatest width equal to that of the central portion of the valve and at the proximal edge of the elevation, their proximal part domed and as tall as the central portion of the valve, distal to this a broad and shallow sulcus extending as far as the elevation. Elevations arising just proximal to the apices, with scarcely any column below the swollen tip, which is semicircular in cross section and as wide as the valve below it; height to the top of the elevations 30–40 μm. A flange-like marginal ridge from elevation to elevation on either side of the valve. Areolae poroid, with a weakly raised external rim, *c.* 0·5 μm in diameter, in interrupted radial rows on the valve surface, areolae 12–15 in 10 μm, rows *c.* 13 in 10 μm, areolae absent from the proximal sulci, present but scattered on the upper part of the mantle at the apices and opposite the central portion of the valve and the domed parts of the projections. Scattered large and stout superficial spines on the central portion of the valve and the domed parts of the projections. Pseudocelli covering the distal half of the tips of the elevations, the areolae in rows meeting at an angle in the centre line of the valve, areolae and rows *c.* 22 in 10 μm. Linking spines 3–4 on each elevation, arising from the middle part only of the proximal margin of the summit of the elevation, concave towards the centre of the valve, acuminate at the tip, *c.* 15 μm long. 4–5 labiate processes close to the centre of the valve.

Middle Eocene (possibly Paleocene or lower Eocene, see p. 284 above). South-western Atlantic, 47° 28.7′ S, 59° 20.6′ W, 1167 m depth. Vema cruise 12, core 46, 630 cm (BM81103, SEM CB4.477–490, CB13.951–960, CB16.609–617, 2133–2154, 4658–4679).

All the specimens of this species that we have seen have consisted of no more than single valves or pairs of sibling valves united by their linking spines. None has any girdle attached. We have seen only a very small number of specimens and the range of size of the species is probably much wider than that given in the description above. The characters that distinguish this species from *Briggera includens*, the other species with a valve of similar outline in valve view, are discussed above (p. 295) under that species.

The material in which this species occurs has a strong admixture of Paleocene and lower Eocene specimens, and hence this species may come from one of those periods rather than the middle Eocene, the age at which the deposit was laid down. However, the specimens are well preserved and show no sign of having been re-worked.

7. **Briggera affixa** (R. Ross) R. Ross & P. A. Sims, **comb. nov.** (Pl. 8 figs 1–6, Pl. 9 figs 1–6)

Hemiaulus affixus R. Ross in *Trans. bot. Soc. Edinb.* **41**: 332, fig. 2 (1972).

Mature frustules with the pervalvar axis equalling or exceeding the apical axis. Valves with a central portion separated from two projections by deep sulci not widening below, the sulci up to *c.* 8 μm wide in the largest specimens; valves 23–90 μm long, 15–33 μm broad, 15–25 μm tall at the centre; central portion of the valve circular to transversely elliptical, highly domed; projections widening very slightly or not at all distal to the sulci, their greatest width about 2/3 that of the central portion of the valve, cuneate with obtuse apices, the portion distal to the sulci as tall as the central portion of the valve. Elevations arising proximal to the apices and inclined distally, 5–11 μm in diameter, their tips sub-spherical and smaller in diameter than the width of the valve below them; height to the top of the elevations 20–48 μm. A flange-like marginal ridge present only opposite the sulci, considerably less high than the central portion of the valve. Areolae poroid, with a weakly raised external rim, *c.* 0·4 μm in diameter, on the valve surface in radial rows 8–15 in 10 μm, with the areolae 8–16 in 10 μm, or areolae scattered and 6–8 in 10 μm, absent at the base of each sulcus, at least proximally; areolae occasionally present on the upper part of the mantle opposite the central dome; a large group of irregularly arranged areolae *c.* 15 in 10 μm at the apex on the upper part of the mantle and the distal side of the elevation. Central portion of the valve and the proximal part of the projections with scattered superficial spines, sometimes very sparse or occasionally apparently absent. Pseudocelli covering all except the proximal side of the tips of the elevations, their areolae in rows radiating from a point close to their distal margin, rows and areolae 24–30 in 10 μm. Linking spines normally 2, occasionally 3, on each elevation, confined to the central part of the proximal side of the summit of the elevation, scarcely concave towards the centre of the valve, not much expanded above, *c.* 5 μm long. No labiate process seen. Each cingulum of a mature frustule consisting of at least 4 open bands, all, except the valvocopula, with well developed ligulae, bands seen 8·5–14 μm deep with areolae in vertical rows, rows 15–16 in 10 μm, areolae 10–12 in 10 μm, and a single row of areolae *c.* 25 in 10 μm close to the advalvar edge of the pars exterior.

Upper Eocene. Kuznetsk, Penza oblast, U.S.S.R. (G. coll. Brun 3075).
'Kamichev', presumed to be Kamyshlov, Sverdlovsk oblast, U.S.S.R. (BM 65797, 65799, 65800 holotype, 65801, 78410, SEM CB16.516–521, CB16.524–533, CB16.748–760, CB16.763–772, CB18.465–470, 1964–1991, 2820–2826, 2952–2954, 3135–3142).
Basin of the River Ob, north-western Siberia, U.S.S.R. (BM SEM CB18.053–063, CB18.072–077).

The information about the girdle of this species comes from two somewhat damaged specimens each consisting of a recently divided frustule with the two daughter sibling valves enclosed within the broken girdle (Pl. 8 fig. 3; Pl. 9 fig. 5). The narrowest bands, about 8·5 μm deep, are probably pleurae.

The differences between this species and *Briggera morenoensis* are discussed above (p. 300) under that species. The other species that it resembles quite closely is *B. robusta*, which also occurs in the upper Eocene of Kuznetsk, Penza oblast, U.S.S.R. That, however, has much broader valves with projections very considerably broader relative to the breadth of the central portion of the valve. Also *B. robusta* has a marginal ridge continuous from one elevation to the other, whereas in *B. affixa* the marginal ridge is interrupted opposite the central portion of the valve.

There is considerable variation in this species between the longer and the shorter specimens. In the longer ones (Pl. 8 figs 1, 2) there is virtually no cylindrical column below the sub-spherical tips to the elevations, whereas in the shorter ones (Pl. 9 figs 1–4, 6) the usually taller, and sometimes much taller, elevations have quite distinct columns below the swollen tips of the elevations. In the very short specimens, also, the elevations arise much nearer the apex, so that such specimens have an outline in girdle view very similar to that of small specimens of *Briggera includens* and *B. siberica*. There is always, however, a slight indentation of the outline below the tip of the elevations in *B. affixa*, but this is never present in *B. includens*; also the elevations are always stouter than those of *B. siberica*. The larger area of denser areolae at the apices also distinguishes *B. affixa* from both these other species.

Briggera affixa is known from the upper Eocene in deposits laid down in the epicontinental seas between Europe and Asia. It has been found in samples of that date from the central Volga basin, the eastern slopes of the Ural mountains and the north-western Siberian lowland, and it may have been present in the latter area over a longer period if our suppositions about the basis of Paramonova's (1964) records of *Hemiaulus sibericus* from there are correct (see above, p. 301).

8. **Briggera robusta** R. Ross & P. A. Sims, **sp. nov.** (Pl. 31 fig. 4)

Valva portione centrali a projecturis duabus separata sulcis profundis centrum valvae versus infra inclinatis, projectura utraque sulco alio basibus elevationum parum proximali traversa, in valvis minimis sulcis duobus in projectura utraque minime separatis; portio centralis valvae transverse elliptica, tholiformis; projecturae prope portionem centralem valvae plerumque parum dilatatae, latitudine maxima sua 4/5 minimum ejus portionis centralis valvae, inde cuneatae apicibus obtusis, inter sulcos duos projecturam utramque transeuntes parum elevatae sed ad bases elevationum fere tam alte quam portio centralis ascendentes; valva 70–140 μm longa, 28–60 μm lata; in specimine uno aspectu cingulari viso ad centrum 32 μm alta. Elevationes apicibus parum proximaliter exorientes, robustae, aspectu valvari circulares; altitudo ad vertices elevationum in specimine uno aspectu cingulari viso 42 μm. Costa marginalis tenuis ab elevatione altera ad alteram in utroque margine valvae, centro valvae opposita non interrupta. Areolae poroides, diametro 1–1·25 μm, prope centrum valvae inordinate dispersae, alibi in superficie valvae in seriebus radialibus interruptis dispositae, seriebus *c.* 7 in 10 μm, areolis 4–7 in 10 μm, in sulcis, in elevationibus, et in limbo, praeter in parte superiore ad apices, ubi multae, et centro valvae oppositae, ubi paucae, carentes. Spinae superficiales nullae. Pseudocelli dimidium distale summorum tumidorum elevationum tegentes, in speciminibus omnibus visis effracti, praeter interdum partem marginalem. Spinae ligantes 4–5, in speciminibus omnibus visis effractae, sed valleculae inter bases eorum deorsum dilatatae. Rimoportula nulla visa.

TYPUS: BM coll. Adams TS693, II, 15, in stratis eocaenicis ad 'Kuznetsk, Penza oblast, U.S.S.R.'

Valve with two projections separated from the central portion of the valve by deep sulci inclined below towards the centre of the valve and crossed by another sulcus a little proximal to the bases of the elevations, in the smallest valves the two sulci on each projection separated by only a very short distance; central portion of the valve transversely elliptical, domed; projections usually widening slightly close to the central portion of the valve, their greatest width at least 4/5 that of the central portion of the valve, distal to this their outline cuneate with obtuse apices, only slightly raised between the two sulci that cross each, but rising to the bases of the elevations almost as high as the central dome; valve 70–140 μm long, 28–60 μm broad, height at the centre of the valve in the one specimen seen in girdle view 32 μm. Elevations arising a little proximal to the apices, stout, circular in cross section; height to the top of the elevation in the one specimen seen in girdle view 42 μm. A flange-like marginal ridge surrounding the valve, except at the apices. Areolae poroid, 1–1·25 μm in diameter, scattered near the centre of the valve, elsewhere on the valve surface in interrupted radial rows, rows *c.* 7 in 10 μm, areolae 4–7 in 10 μm, absent from the troughs of the sulci, from the elevations and from the mantle, except for a large group on the upper part at each apex and a smaller group opposite the central portion of the valve. No superficial spines. Pseudocelli on the distal half of the tips of the elevations, broken away, except for their margins, in all the specimens seen. Linking spines 4–5, broken away in all specimens seen but the grooves between their bases widening downwards. No labiate process seen.

Upper Eocene. Kuzentsk, Penza oblast, U.S.S.R. (BM 32739, coll. Adams TS693; G coll. Brun 3074, 3075).
Rostov, U.S.S.R. (for this locality see p. 281). (BM 81104.)

There are ten specimens of this species on the five microscope slides listed above and we have examined these with the light microscope. No unmounted specimens that could be examined with the scanning electron microscope have been available to us. All the specimens that we have seen consist of single valves and the preservation is rather poor; in all of them the greater part, at least, of the pseudocelli is broken away and so are the linking spines. Although the information that is provided by the specimens that we have seen is incomplete, it is sufficient to show that they represent a species of *Briggera* distinct from any of the others; the way in which the grooves between the bases of the linking spines widen downwards shows that these were interlocking, and on some specimens enough of the margin of the pseudocelli remains to show that these were present. The areolae in all the specimens are considerably larger than those in most, but not all, species of the genus; although preservation is poor, we do not believe that this is entirely due to their being enlarged by erosion. Whilst we are not able to give as full a description of this species as of the others introduced as new in this account, we have seen enough specimens to provide one that is an adequate basis for publishing it as a new species.

Briggera robusta resembles both *B. morenoensis* and *B. affixa* in outline but differs from both in the greater width of the projections relative to that of the central portion of the valve, in the absence of superficial spines, and in the greater size of its areolae. It also differs from *B. affixa* in that its marginal ridge is continuous on either side of the valve from one elevation to the other. From *B. capitata*, the other species with deep sulci and large areolae, it differs in the outline of the projections and also in the lesser extent by which its elevations exceed its central portion.

Briggera robusta has been found in the fossil deposit from Kuznetsk, Penza oblast, U.S.S.R., first studied by Pantocsek (1889). According to Glezer (in Glezer et al., 1974) this is most probably of upper Eocene age, and this is the age attributed to the material from Rostov in which it also occurs.

9. **Briggera caverna** (Brun) R. Ross & P. A. Sims, **comb. nov.** (Pl. 31 fig. 5a, b)

Hemiaulus caverna Brun in *Mem. Soc. Phys. Hist. nat. Genève* **31** (2): 31, t. 12 fig. 7 (1891).

Valve subhexagonal, the margins opposite the centre shorter than the other sides and concave, the centre portion domed and bounded by two deep transverse sulci; the valve strongly inflated distal to the sulci, the bases of the elevations being higher than the central dome; valves 70–100 μm long, 48–55 μm broad, *c.* 30 μm tall at the centre. Elevations arising somewhat proximal to the apices, inclined outwards, their stems below the swollen tip short, *c.* 7 μm tall; height to the top of the elevations *c.* 60 μm, the swollen tips transversely elliptical in cross section, 20–27 μm × 16–20 μm. A flange-like marginal ridge running from one elevation to the other on either side of the valve, slightly taller than the centre of the valve. Areolae 0·7–1·0 μm in diameter, on the central portion radiating in short and irregular rows from a hyaline central area *c.* 5 μm in diameter to form a transversely elliptical patch *c.* 12·5 × 30 μm, perhaps sometimes larger, rows and areolae 6–10 in 10 μm, the remainder of the central portion hyaline; areolae on the valve distal to the sulci in rows converging towards the elevations, spacing as on the central portion; a large and dense patch of areolae on the upper part of the mantle at the apices, mantle elsewhere hyaline. Pseudocelli broken away on the specimens seen but apparently covering the summit of the elevations and the upper part of the distal side of their tips. Linking spines 3–4, on the central part of the proximal edge of the elevations, all broken off in the two specimens seen but the grooves between them widening downwards. No labiate process seen.

Upper Eocene, Kuznetsk, Penza oblast, U.S.S.R. (G coll. Brun 3074, 3075, syntypes; Brun, 1891).

The above description is based on three specimens, two of them, one the holotype, mounted in valve view the third in girdle view. It is considerably less adequate than the descriptions we have been able to provide of the other species of this genus, but the three specimens available to us are sufficient to show that this species, originally described by Brun (1891), has all the characteristics of *Briggera*. It has, however, an outline very different from that of any other species of the genus. It is apparently very rare in the upper Eocene deposit from Kuznetsk, Penza oblast, U.S.S.R., and it has not been found anywhere else.

10. **Briggera ornithocephala** (Grev.) R. Ross & P. A. Sims, **comb. nov.**

Hemiaulus ornithocephalus Grev. in *Trans. microsc. Soc. Lond.* II, **13**: 32, t. 3 fig. 16 (1865); Grove & Sturt in *J. Quekett microsc. Club* II, **3**: 11, t. 6 figs 18, 19 (1887); A. Schmidt, *Atlas Diat.*: t. 142 figs 34, 36, 37 (1889); J. D. Möller, *Lichtrucktaf. herv. schöner vollst. Möller'scher Diat.-Präp.: t. 6 row 2 fig. 4, t. 26 row 6 figs 16–18 (1891), Verz. Lichtdrucktaf. Möll. Diat.-Präp. enth. Arten*: 42, 165 (1892); Wise in *Ann. Mag. nat. Hist.* XII, **5**: 405, t. 20 figs 3–5 (1952); R. Ross in *Trans. bot. Soc. Edinb.* **41**: 335, fig. 4 (1972).

Biddulphia virgata Grove & Sturt in *J. Quekett microsc. Club* II, **2**: 325, t. 18 fig. 11 (1886).

Kittonia virgata (Grove & Sturt) Grove & Sturt in *J. Quekett microsc. Club* II, **3**: 75 (1887), excl. t. 6 fig. 23.

Hemiaulus virgatus (Grove & Sturt) Fuge in *Watson's Microsc. Rec.* **40**: 13, figs 1–4 (1937), excl. fig. 5.

Valves elliptical, 15–115 μm long, 12–80 μm broad, 5–40 μm tall at the centre, crossed by two shallow and inconspicuous sulci or, in the smallest specimens, by only one sulcus, the portions distal to the sulci (or sulcus) inflated. Elevations arising proximal to the apices of the valve, cylindrical or tapering slightly upwards below the swollen spherical tip; height to the top of the elevations 30–90 μm. A flange-like marginal ridge extending around the whole valve or sometimes interrupted at the apices, *c.* 2·5–6 μm tall opposite the central part of the valve. Areolae poroid, *c.* 0·3 μm in diameter; on the central part of the valve usually in irregular radial rows, rows 5–8 in 10 μm, areolae 5–14 in 10 μm, occasionally only two patches of scattered areolae, one on either side of the valve centre, even more rarely central part of the valve hyaline; areolae on the valve surface distal to the sulci in irregular rows converging towards the elevations, rows 8–10 in 10 μm, areolae 8–14 in 10 μm; scattered areolae also present on the apical part of the mantle; a somewhat irregular vertical row of small areolae usually present on the distal face of the elevations. Scattered superficial spines occasionally present but usually absent. Pseudocelli on the distal half of the tips of the elevations, their areolae in rows radiating from a transverse line in the centre of the pseudocellus, rows and areolae 18–22 in 10 μm. Linking spines 3–4 on each elevation, very slightly concave towards the centre of the valve, only slightly or not at all expanded above, their apices acute. No labiate process seen. Valvocopula (presumed) an open band, its pars exterior *c.* 20 μm deep, with poroid areolae in interrupted vertical rows, rows 12–13 in 10 μm, areolae 6–7 in 10 μm, pars interior hyaline, *c.* 3 μm deep.

subsp. **ornithocephala** (Pl. 10 figs 1–8)

Valve 5–12 μm tall at the centre, central portion of the valve flat or raised only 1–2 μm higher than the top of the mantle, height to the summit of the elevations 30–55 μm; vertical row of areolae always present on the distal face of the elevations.

Middle Eocene. Cambridge Estate, Barbados (BM 3263 holotype; Greville, 1865*a*).

Middle Eocene – lower Miocene. Chalky Mount, Barbados (BM coll. Adams GC1617).

Upper Eocene. Oamaru, New Zealand (BM 9392, 9395, 11126, 30848, 35668 (Allan's Farm), 35916 (Papakaiyo, lower), 36097 (Forrester's Hill), 36299 (Allan's Farm), 38249 (Forrester's Hill), 38252 (Forrester's Hill), 38253 (Totara), 46559, 46577, 46596, 46623, 46632, 46636, 52767, 60783, 60784, 63891 (Bain's Farm), 70120, 74059 (Papakaiyo), 74060 (Papakaiyo), 74062 (Jackson's Paddock), 76321, 76322, 77033, coll. Adams A911 (Cormack's Siding), Bess. 299, Bess. 672 (Railway Cutting), D960, G104 (Cormack's Siding), G132 (Troublesome Gulley, upper), G591, GC1618, GC1619, GC2792, J333, J880, J1029 (Jackson's Paddock), TS23, TS199, TS270, TS271, TS272 (Jackson's Paddock), TS289, TS292; SEM CB7.076, CB9.268–272, CB10.077–093, CB10.136, CB16.537–550, CB16.553–556, CB16.842–846, 2113–2120, 2169–2182, 2754–2763, 3979–3980; PH coll. Shulze arr. 801, 1913, 1914, Gen. coll. 89160 (Borries); Grove & Sturt, 1886, 1887*a*; A. Schmidt, 1889; Fuge, 1937; Wise, 1952).

subsp. **atlantica** R. Ross & P. A. Sims, **subsp. nov.** (Pl. 11 figs 1–7, Pl. 12 figs 1–7, Pl. 31 figs 6, 7)

Valva ad centrum 18–40 μm alta, portione centrali convexa et 5–20 μm altiore quam limbo, altitudo ad vertices elevationum 55–90 μm; series verticalis areolarum plerumque sed non semper in latere distali elevationum.

TYPUS: BM 81105, ex stratis eocaenicis de profundis maris Atlantici australis.

Valve 18–40 μm tall at the centre, its central portion convex and 5–20 μm taller than the mantle, height to the summit of the elevations 55–90 μm; vertical row of areolae usually but not always present on the distal face of the elevations.

Middle Eocene. South-western Atlantic, 51° 08′ S, 54° 22′ W, 1525 m depth, Vema cruise 17, core 107, 50 cm (BM 81107), 120 cm (BM SEM 2608–2629, 2731–2735).

Middle-upper Eocene. South-western Atlantic, 53° 01′ S, 52° 52′ W, 2880 m depth. Vema cruise 18, core 104, 330 cm (BM 81105, SEM CB11.831–834, CB19.103–107, CB19.119–123, CB19.711–719, 2377–2395, 2592–2598, 3239–3245, 3252–3265, 3451–3471, 3477–3480, 3940–3970, 4381–4408).

South-western Atlantic, 47° 45.7′ S, 57° 38.5′ W, 3650 m depth. Conrad cruise 12, core 237 (BM 81106).

We have seen no specimens of a complete frustule of this species but only single valves or pairs of sibling valves joined by their interlocking linking spines. In a few specimens consisting of two joined sibling valves, including one that we have examined with the scanning electron microscope, there is a single girdle band around one valve or one around each of the two valves of the pair. The position of the pars interior of these bands shows that they are not part of the cingulum of the theca to which the valve they surround belongs but part of the epicingulum of the frustule of which it is the hypovalve. As the bands are open and without ligulae, we interpret them as valvocopulae. A specimen (Pl. 10 figs 5–7) examined under the scanning electron microscope has one such band around each valve, and the gap between them, presumably once occupied by the remainder of the girdle of the parent cell, is 65 μm. This specimen belongs to subsp. *ornithocephala*.

As is pointed out above (p. 292), the name *Hemiaulus ornithocephalus* has been widely misapplied to both *Briggera includens* and *B. capitata* as well as being used in its correct sense. In their treatment of the diatoms from the late upper Eocene deposit at Oamaru, New Zealand, Grove & Sturt (1886, 1887*a, b*), however, did not include *B. ornithocephala* and *B. capitata* in one species but misidentified *B. capitata* as *B. includens*. Nevertheless, they did not recognize a specimen of *B. ornithocephala* seen in valve view for what it was but described it as a species of *Biddulphia, B. virgata*. However, when they later established the genus *Kittonia* Grove & Sturt and transferred *Biddulphia virgata* to it, they illustrated the new combination by a figure of another species, a fact that was pointed out by Wise (1952), who described this latter species as *Biddulpha sturtii* Wise, a later synonym, we suggest, of *Biddulphia podagrosa* Grev. (see p. 317). Fuge (1937) recognized that the name *Biddulphia virgata* applied to this species, but considered that *Hemiaulus ornithocephalus* did not; he presumably thought that the latter name applied to *B. capitata* as most specimens of that species in collections are so named. However, one of the five micrographs that he provided when making the new combination *Hemiaulus virgatus* (Grove & Sturt) Fuge is of *B. novocastrensis* (R. Ross) R. Ross & P. A. Sims, not of *B. ornithocephala*.

The species that is closest to *Briggera ornithocephala* in most respects is *B. novocastrensis*, which has a valve of very similar shape, but much larger areolae, rather stouter elevations, and pseudocelli divided by a vertical space bearing very few areolae, and it lacks a vertical row of areolae on the distal face of the elevations. Such a row of areolae is present on the imperfectly known *Briggera* sp. I from the Campanian (upper Cretaceous) of the northern Ural mountains but this has a rather different outline and deeper sulci; also its elevations arise at the apices rather than somewhat proximal to these, and they have no columnar part below the swollen tip. *B. paratethyos* R. Ross & P. A. Sims also has a vertical row of areolae on the distal side of the elevation, but it too has elevations inserted at the apex with the columnar part inclined inwards; also its flange-like marginal ridge is much deeper than that of *B. ornithocephala* and there are probably differences in its linking spines.

The specimens from the cores taken in the south-western Atlantic are more robust than those from Barbados and Oamaru, New Zealand. Their valves are much deeper and their elevations larger in diameter, and they can be considerably larger in valve view, attaining a length of up to 115 μm, as against a maximum of 75 μm for those from Barbados and New Zealand. Because of the much greater depth of the valve itself and the greater stoutness of the elevations in the Atlantic specimens, the elevations of these do not appear to exceed the central part of the valve to any greater extent than those of the Barbados and New Zealand specimens even although their total height is considerably more. In the largest of the Atlantic specimens the columnar part of the elevations below the swollen tip is only about 12 μm tall and on these specimens there is no vertical row of areolae on their distal face, although this is present on the smaller specimens. In our view the differences between these populations are sufficient for separation at the infraspecific, but not the specific, level, and as the two taxa occur in separate geographical areas and are perhaps not contemporary, the subspecies seems to be the appropriate level.

The smaller valves of *Briggera ornithocephala* subsp. *ornithocephala* with only a single sulcus between the elevations have somewhat deeper mantles than the larger ones with two sulci. The height of the valve centre in these specimens is 9–10 μm, but this is at the base of the sulcus rather than at the top of the somewhat raised central part present in the larger valves. The largest specimen with a single sulcus that we have seen had an apical length of 34 μm.

Superficial spines were present on only one specimen of subsp. *ornithocephala*, that from Chalky Mount, Barbados, which was mounted by W. A. Firth, a professional mounter active at the end of the nineteenth century. This may come from any level within the Oceanic Beds, which cover a period from the middle Eocene to the lower Miocene. One therefore cannot tell whether this specimen is contemporary with, earlier than, or later than, those from other localities and without such spines. Also, one of the six specimens of subsp. *atlantica* that we have seen has superficial spines. Until more information becomes available about the distribution in time and space of specimens with and without superficial spines, there is no adequate justification for basing any taxonomic separation on their presence or absence.

The species is apparently rare in the deposits from Barbados in which it has been found and also in the middle-upper Eocene material from the south-western Atlantic. In the late upper Eocene of Oamaru, New Zealand, on the other hand, it is not uncommon.

Grunow (1884: 62) concludes a short remark on *Hemiaulus ornithocephalus* with: 'Eine sehr ähnliche, unregelmässig zart punktirte Form, die ich als var. Nicobarica bezeichne, fand ich im Polycisten-Gestein von Nancoori.' We have, however, seen no specimen of *Briggera* from the Miocene deposits of the Nicobar Islands, nor has any figure of one been published; the specimen on which Grunow based this remark is not in his collection. Whether the genus is represented in these deposits and, if so, whether by *B. ornithocephala* or by some other species must therefore remain an open question.

11. **Briggera bonei** R. Ross & P. A. Sims, **sp. nov.** (Pl. 13 figs 1–8, Pl. 31 fig. 8)

Frustula axe pervalvari ad 5-plo longiore quam axe apicali. Valva elliptica ad subcircularis, 32–115 μm longa, 25–70 μm lata, ad centrum 15–35 μm alta, sulcis duobus inconspicuis et non profundis aut, in speciminibus minoribus, sulco uno traversa, superficie valvae inter sulcos minime elevata, sulcis distali valde inflata. Elevationes apicibus parum proximaliter exorientes, summis subglobosis in portionibus distalibus inflatis valvae sessilibus, verticibus nonnumquam parum depressis; altitudo ad vertices elevationum 32–70 μm. Costa marginalis tenuis ab una portione distali inflata valvae ad alteram exstensa, inter sulcos vel sulco uno opposita minus alta quam alibi. Areolae poroides, extrinsecus margine elevato, diametro 0·7–1·5 μm, sed paucissimae minores, diametro *c.* 0·3 μm, in superficie valvae et in parte superiore limbi prope apices inordinate dispersae, nonnumquam prope marginem valvae in seriebus radialibus interruptis, 2·5–4·5 in 10 μm; aliquando una vel duae areolae in parte superiore limbi centro valvae opposita. Spinae superficiales nullae. Pseudocelli dimidium distali summi utraeque elevationis tegentes, areolis suis *c.* 18 in 10 μm, in seriebus ab centro marginis inferioris utrique pseudocelli radiantibus. Spinae ligantes in utraque elevatione 2–4, ad partem centralem lateris proximalis verticis elevationis limitatae, centrum valvae versus parum concavae, supra valde expansae, apicibus acutis, *c.* 7 μm longae. Rimoportula non visa. Valvocopula ad unum apicem frustuli aperta, *c.* 13 μm profunda, areolis multo minoribus quam eis valvae, dispersis, 5–7 in 10 μm; taenia plus abvalvaris (? pleura) *c.* 17 μm profunda, ligula bene effecta, serie una areolarum 12–13 in 10 μm secus marginem advalvarem partis exterioris, vitta hyalina abvalvari *c.* 5 μm lata, alibi areolis dispersis 5–7 in 10 μm, diametro 0·3–0·4 μm. TYPUS: BM 78447, ex stratis eocaenicis de profundis maris Atlantici australis.

Frustules with the pervalvar axis up to five times as long as the apical axis. Valve elliptical to sub-circular, 32–115 μm long, 25–70 μm broad, 15–35 μm tall at the centre, crossed by two shallow and inconspicuous sulci between which the valve surface is scarcely raised, or, in the smaller specimens, by a single sulcus, the portions distal to the sulci strongly inflated. Elevations arising slightly proximal to the apices with sub-globular tips sessile on the inflated distal portion of the valve, their upper surfaces sometimes shallowly depressed, height to the top of the elevations 32–70 μm. A flange-like marginal ridge on either side of the valve extending from one inflated distal portion of the valve to the other but absent around the apices, its upper margin lower between the sulci or opposite the single sulcus than elsewhere. Areolae poroid, with a raised external rim, 0·7–1·5 μm in diameter, but a very few smaller, *c.* 0·3 μm in diameter, irregularly scattered over the valve surface and on the upper part of the mantle in the apical parts of the valve, sometimes in interrupted radial rows near the margin of the valve, 2·5–4·5 in 10 μm; one or two occasionally present on the upper part of the valve mantle opposite the valve centre. No superficial spines. Pseudocelli on the distal halves of the tips of the elevations, their areolae *c.* 18 in 10 μm, arranged in rows radiating from a point in the centre of their lower margin. Linking spines 2–4 on each elevation, arising from the central part only of the proximal edge of the summit of the elevations, very slightly concave towards the centre of the valve, strongly expanded above, acute at the apex, *c.* 7 μm long. No labiate process seen. Valvocopula an open band, *c.* 13 μm deep, the opening at one apex of the frustule, with scattered areolae 5–7 in 10 μm, much smaller than those of the valve; a more abvalvar girdle band (? pleura) *c.* 17 μm deep with a well developed ligula, a single row of areolae 12–13 in 10 μm along the advalvar edge of its pars exterior, the abvalvar 5 μm hyaline, the rest with scattered areolae 5–7 in 10 μm, the areolae 0·3–0·4 μm in diameter.

Middle Eocene. South-western Atlantic, 51° 08′ S, 54° 22′ W, 1525 m depth. Vema cruise 17, core 107, 120 cm (BM 78446, 78447).

Middle-upper Eocene. South-western Atlantic, 53° 01′ S, 52° 52′ W, 2880 m depth. Vema cruise 18, core 104, 330 cm (BM 81108 SEM CB11.815–823, CB16.599–605, CB16.607–608, CB19.108–110, CB19.112–118, CB19.720–721, 2396–2409, 2512–2519, 2576–2591, 2599, 3250–3251, 3472–3474).

This species is named after Mr E. C. P. Bone of Portslade, Sussex, who mounted the type specimen, and who has given us much help over the years by providing us with selected specimens of genera we have been studying.

The smaller specimens of this species that are crossed by only a single sulcus resemble very closely the smallest specimens of *Briggera capitata* (Grev.) R. Ross & P. A. Sims, but in that species there is apparently always a central dome, which may be very small, and at least a slight indentation of the outline opposite the sulci. The other species which, like *B. bonei*, have an elliptical outline and large areolae, i.e. *B. novocastrensis* (R. Ross) R. Ross & P. A. Sims and *B. haitensis* (R. Ross) R. Ross & P. A. Sims, have elevations with a columnar part below their swollen tips and pseudocelli divided by an almost hyaline vertical space. No specimens of either of these with a single sulcus have been found, but it would seem that the majority of specimens of *B. bonei* from the South Atlantic cores are of that type.

12. **Briggera haitensis** (R. Ross) R. Ross & P. A. Sims, **comb. nov.** (Pl. 14 figs 5–8, Pl. 31 fig. 9)

Hemiaulus haitensis R. Ross in *Trans. bot. Soc. Edinb.* **41**: 339, fig. 6 (1972).

Hemiaulus ornithocephalus sensu Truan & Witt, *Diat. Polycyst. Jérémie, Haiti*: 16, t. 3 figs 18–20, 24–25 (1888), non Grev.; J. D. Möller, *Lichtdrucktaf. herv. schöner vollst. Möller'scher Diat.-Präp.*: t. 6 row 2 fig. 5, t. 16 (I) row 6 figs 10–11 (1891), *Verz. Lichtdrucktaf. Möll. Diat.-Präp. enth. Arten*: 42, 112 (1892).

Valve broadly elliptical to subcircular, 45–70 μm long, 40–55 μm broad, 30–45 μm tall at the centre, crossed by two shallow and inconspicuous sulci, the whole valve in the form of a high dome. Elevations arising somewhat proximal to the apices of the valve, stout and transversely elliptical in cross section, swollen above; height to the top of the elevations 50–70 μm. A slight marginal ridge surrounding the whole valve. Areolae poroid, with a weakly raised rim externally, 1·0–1·5 μm in diameter, irregularly scattered over the valve surface except in the sulci, 2·5–5 in 10 μm, extremely few or absent on the mantle and very few on the elevations. No superficial spines. Pseudocelli covering the distal side of the swollen tips of the elevations, divided by an almost hyaline vertical space, their areolae 14–18 in 10 μm. Linking spines 3–4, on the proximal side of the summits of the elevations, concave towards the centre of the valve, not much expanded above, acute at the tips, *c.* 22 μm long. No labiate process seen.

Middle Eocene? Conset, Barbados (BM SEM CB11.363–367, CB11.567–575, CB13.500). For the date of this material see p. 283 above.

Middle Eocene — lower Miocene. Barbados (PH coll. Febiger 203, coll. Shulze arr. 3095).

Lower Miocene ? Jérémie, Haiti (BM 38251 holotype, coll. Adams D962, J1099, TS220, TS222, TS543 SEM B13.475–480, B13.482–485, 3165–3175; PH coll. Boyer Q-6-8; Truan & Witt, 1888; Möller, 1891, 1892). For the date of this material see p. 283 above.

All the specimens of this species that we have seen consist either of single valves or of pairs of sibling valves held together by their interlocking linking spines. No girdle elements have been present on any of them.

Briggera haitensis differs from *B. novocastrensis* both in the profile of the valve and in the presence of some scattered areolae in the apical region on the upper part of the mantle and the valve surface just above it. We regard these differences as a sufficient basis for considering the two as separate species, although we should be more confident of this if a larger number of specimens were available.

It would seem from the number of specimens present in the collections at BM that this species is not uncommon in the deposit at Jérémie, Haiti, but it seems to be rarer in material from Barbados. As we have pointed out earlier (p. 283) the diatom evidence about the relative dates of the deposits from Conset, Barbados and Jérémie, Haiti, is inconsistent with that from the radiolaria. The locality of the specimens of this species in coll. Febiger and coll. Shulze at PH is given as 'Barbados' with no further detail, and there is thus no indication of the level within the Oceanic Beds from which they came. We are accordingly not able to make any firm statement about the span of geological time during which this species existed.

13. **Briggera novocastrensis** (R. Ross) R. Ross & P. A. Sims, **comb. nov.** (Pl. 14 figs 1–4, Pl. 31 fig. 10)

Hemiaulus novocastrensis R. Ross in *Trans. bot. Soc. Edinb.* **41**: 338, fig. 5 (1972).
Hemiaulus ornithocephalus sensu J. H. Robinson in *J. Barbados Mus.* **4**: 10 (1936), non Grev.
Hemiaulus virgatus Fuge in *Watson's Microsc. Rec.* **40**: 13 (1937) pro parte, quoad fig. 5.

Frustules with the pervalvar axis two to three, possibly more, times as long as the apical axis. Valve broadly elliptical to subcircular, 35–85 μm long, 8–14 μm tall at the centre, crossed by two shallow sulci, not domed at the centre, but the parts distal to the sulci rising abruptly to the base of the elevations. Elevations arising slightly proximal to the apices, stout and transversely elliptical in cross section, swollen above; height to the top of the elevations 40–60 μm. A flange-like marginal ridge extending around the whole valve, except at the apices, 1–2 μm deep opposite the central part of the valve. Areolae poroid, 1·0–1·5 μm in diameter, irregularly scattered over the valve surface, 3–5 in 10 μm, absent from the mantle and from the elevations, except for a few on their proximal side near the top. No superficial spines. Pseudocelli covering the distal halves of the tips of the elevations, divided by an almost hyaline vertical space, areolae 16–18 in 10 μm. Linking spines usually 2, on the proximal side of the summits of the elevations, not much expanded above. No labiate process seen. Each cingulum consisting of at least two elements, probably more; valvocopula with a pars exterior *c.* 30 μm deep having a line of poroid areolae *c.* 1 μm in diameter and 5·5–6 in 10 μm close to the advalvar edge and similar areolae scattered over the remainder, 3–4 in 10 μm, and with a hyaline pars interior *c.* 6 μm deep. Another girdle band (? pleura) with a pars exterior *c.* 20 μm deep having a line of areolae *c.* 9 in 10 μm close to the advalvar edge and elsewhere areolae in interrupted vertical rows, rows 8 in 10 μm, areolae 3–4 in 10 μm, and a hyaline pars interior *c.* 5 μm deep.

Middle-upper Eocene boundary. Indian Ocean, 10° 25′ S, 63° 15′ E, 3115 m depth, dredge sample. Dodo-123-D1 (BM SEM CB11.410–417, CB16.577–586).

Upper Eocene — lower Miocene. Newcastle, Barbados (BM 41187 holotype, coll. Adams TS833 (Clarke's Cliff); Robinson, 1936*b* (Clarke's Cliff)).

Only three specimens of this species have been seen. The one from the Indian Ocean examined with the scanning electron microscope is a single valve and one of the two from Barbados consists of a pair of sibling valves joined by their interlocking linking spines but without any girdle elements. The type specimen, however, which is also from Barbados, consists of a pair of linked sibling valves and a third valve with its margin in contact with that of one of this pair, together with some girdle elements (Pl. 31 fig. 10). This is presumably a pair of frustules very shortly after cell division with one of the valves of the parent frustule lost and also some parts of the girdle. A valvocopula is still attached to the epivalve of the daughter cell with two valves present and there is a similar band around the valve at the other end of the specimen. Between these two valvocopulae but separated from them by gaps of 10 μm and 20 μm are two bands, one overlying the other, the two surrounding the upper parts of the elevations of the linked sibling valves. It is these latter bands that are described as the possible pleurae and we assume that between them and the valvocopulae there were originally other bands that have been lost. The specimen is mounted in girdle view and it is impossible to say whether or not any of the girdle bands are open at one apex, as is normal in the genus. However, no trace of a ligule could be detected on the bands that are thought to be pleurae.

Examination of the specimen from the Indian Ocean with the scanning electron microscope showed that it had divided pseudocelli resembling those of *Briggera haitensis* (R. Ross) R. Ross & P. A. Sims, and also that there were a few areolae on the proximal side of the elevations. Neither of these features was mentioned in the original description of the species but re-examination of the type specimen showed that they are present but were overlooked when the previous account was being prepared.

There is no vertical row of areolae on the distal side of the elevations. This, together with the stouter elevations and the divided pseudocelli provides sufficient evidence that this is a species separate from *Briggera ornithocephala* (Grev.) R. Ross & P. A. Sims and that it is not based on eroded specimens of that species in which the areolae have become enlarged.

The Indian Ocean specimen of this species came from a dredge sample of material from the middle-upper Eocene boundary. The age of the two specimens from Newcastle, Barbados, is much less certain, but it is probably upper Eocene or later (see p. 284 above). Robinson's (1936*b*) record of *Hemiaulus ornithocephalus* from Clarke's Cliff, Newcastle, is based on the specimen of *Briggera novocastrensis* on BM coll. Adams TS833.

Fuge (1937), when publishing the combination *Hemiaulus virgatus* (Grove & Sturt) Fuge for *Briggera ornithocephala*, illustrated the name with five micrographs, one of which, his fig. 5, is of *B. novocastrensis*. He made no definite statement of the locality from which the specimen depicted in this figure came but implied that all his illustrations were of specimens from Oamaru, New Zealand. As there is no other record of *B. novocastrensis* from there nor any specimen in the collections we have examined, we think this an inadequate basis for including the late upper Eocene of Oamaru, New Zealand, in the distribution of the species.

14. **Briggera paratethyos** R. Ross & P. A. Sims, **sp. nov.** (Pl. 15 figs 1–6, Pl. 32 figs 1, 2)

Valva elliptica, apicibus subacutis obtusisve, 55–100 μm longa, 40–67 μm lata, sulcis duobus non valde profundis vel, in speciminibus minoribus, uno traversa, inter eos valva parum elevata, sed sulcis vel sulco distalis inflata et bases elevationum versus valde elevata. Elevationes apice valvae exorientes, partibus suis inferioribus columnaribus introrsum parum inclinatis, summis distaliter parum, lateraliter et proximaliter valde, tumidis; altitudo ad vertices elevationum 50–90 μm, diameter summorum 22–30 μm. Costa marginalis tenuis alta totam valvam praeter apices circuiens, 8 μm minimum altior quam portio centralis valvae. Areolae poroides, extrinsecus margine parum elevato, diametro 0·2–0·4 μm, inter sulcos inordinate dispersae et *c.* 7 in 10 μm vel magis sparsiores, sulcis distales in seriebus interruptis elevationes versus convergentibus, seriebus 10–12 in 10 μm, areolis 12–14 in 10 μm; in elevationibus nullae praeter, nonnumquam, seriem verticalem brevem in latere distali; in limbo nullae praeter, nonnumquam, paucissimas ad apices in parte superiore. Spinae superficiales nullae. Pseudocelli vertices et dimidia distalia summorum elevationum tegentes, areolis suis in seriebus ex spatio hyalino parvo ad limitem distalem verticis elevationis posito radiantibus, areolis et seriebus *c.* 16 in 10 μm. In latere proximali verticis utrisque elevationis prominentia labelliformis, 9–11 μm lata, in speciminibus omnibus visis margine libero, ut videtur, fracto. Rimoportula non visa.

TYPUS: BM 81109, ex stratis miocaenicis ad 'Pouzdřany, Czecho-Slovakia'.

Valve elliptical, with subacute to obtuse apices, 55–100 μm long, 40–67 μm broad, crossed by two rather shallow sulci, or, in the smallest specimens, only one, the valve not much raised between the sulci but the portions distal to the sulci or sulcus inflated and rising strongly to the bases of the elevations. Elevations arising at the apices of the valve, their lower columnar parts inclined slightly towards the centre of the valve, their tips swollen only slightly distally but strongly both laterally and proximally. Height to the top of the elevations 50–90 μm, diameter of the tips 22–30 μm. A deep flange-like marginal ridge extending around the whole valve except at the apices, exceeding the central portion of the valve by at least 8 μm. Areolae poroid, with a weakly raised external rim, 0·2–0·4 μm in diameter, between the sulci irregularly scattered and *c.* 7 in 10 μm to very sparse, distal to the sulci in interrupted rows converging towards the elevations, rows 10–12 in 10 μm, areolae 12–14 in 10 μm, absent on the elevations, except sometimes for a short vertical row on their distal side, and on the mantle except sometimes for a very small number on the upper part at the apices. No superficial spines. Pseudocelli covering the summits and the distal half of the swollen tips of the elevations, their areolae in rows radiating from a small hyaline space at the distal edge of the summit of the elevation, rows and areolae *c.* 16 in 10 μm. On the proximal side of the summit of each elevation a labelliform projection 9–11 μm wide with signs of fracture on its free edge in all specimens seen. No labiate process seen.

Lower Miocene. Pouzdřany (formerly Pausram) Czechoslovakia (BM 81109, SEM CB18.512–513, CB18.519–545, 2884–2897, 3744–3760).

As the specific epithet for this species we have used, in its genitive form, the name of the Miocene sea in whose sediments the species was deposited.

We have seen single valves only of this species. These all have flattened tops to their elevations and a lip-like projection on the proximal side of these. On the free edge of this projection there are what may be the broken bases of interlocking spines, but these are far from clear. Nevertheless, the species has all the other characteristics of *Briggera*. Also most specimens of it share with *B. ornithocephala*, the species it most closely resembles in other respects, the character of having a vertical row of areolae on the distal face of the elevation below the pseudocelli; this character is also present in the imperfectly known *Briggera* sp. I. The small hyaline area in the centre of the pseudocellus is not present in any other member of the genus, but both *B. novocastrensis* and *B. haitensis* have pseudocelli completely divided by a vertical almost hyaline space.

This species occurs later in the fossil record than any other member of the genus, except perhaps *Briggera haitensis*, and its close resemblance to *B. ornithocephala* suggests that it may be an evolutionary successor of that species.

Briggera sp. I (Pl. 16 figs 1–7)

Valve sub-rhombic, rounded at the apices and opposite the centre of the valve, the margin slightly indented opposite two deep transverse sulci situated midway between the valve centre and the apices; valve slightly depressed at the centre, 92 μm long, 60 μm broad. Elevations arising at the apices, transversely elliptical in cross section, not very tall, with no column below the swollen tip. A flange-like marginal ridge surrounding all the valve except at the apices. Areolae with a slightly raised rim externally, irregularly scattered over the valve surface and on the mantle in the apical region, 2–4 in 10 μm. A vertical row of areolae at the apex on the upper part of the mantle and the lower part of the elevation, the row sometimes double or triple over part of its length. Scattered superficial spines on the valve surface between the sulci but not distal to them. Pseudocelli on the distal side of the swollen tips of the elevations, their areolae in rows radiating from a point near their lower margin, rows and areolae *c.* 22 in 10 μm. Linking spines 3–4.

Upper Cretaceous — Campanian. Exposure XI (14), near Til'tim, basin of the river Synya, Tyumen'sk oblast, U.S.S.R. (BM SEM CB17.540–553, 2908–2916, 3714–3735).

The description given above is based on a single specimen examined with the scanning electron microscope and consisting of only a single valve with broken linking spines. It is nevertheless clearly a representative of a species of *Briggera*; the shape of the grooves between the broken bases of the linking spines shows that these were interlocking (Pl. 16 fig. 7), and it has all the other characters of the genus. On the other hand, it is too different from the examples of any of the other species for it to be regarded as possibly falling within their range of variation. Because we have not been able to find another specimen that we could mount for light microscopy and designate as a holotype, and also because a description based on a single specimen of a diatom cannot, in our view, be an adequate basis for the publication of a new species, we have not given this ~~one~~ a name.

This diatom is intermediate in outline both in valve and girdle view between the species with deep sulci and projections sharply delimited from the central portion and those with shallow sulci and elliptical valves. It shares, however, with *Briggera ornithocephala* and *B. paratethyos*, both members of the latter group, the character of having a vertical row of areolae on the upper part of the mantle and the lower part of the elevation at each apex (Pl. 16 fig. 4). It is the possession of this character that convinces us that it should be grouped with these species. They are of Middle to late Eocene and Miocene age respectively and it is tempting, therefore, to suggest an evolutionary progression from *Briggera* sp. I through *B. ornithocephala* to *B. paratethyos*. There is nothing in their morphology to indicate that this might not be correct.

Biddulphia podagrosa Grev. (Greville, 1866: 82, pl. 9 fig. 17) is a species with stout elevations and large pseudocelli. It was transferred to *Hemiaulus* by Grunow (1884: 65) as *H. podagricus* without comment, and Wise (1952: 407) remarks that both the specimens in Greville's collection (BM 3054, 3072) 'bear some evidence of broken-off mucros.' It might therefore be thought that this is probably another species of *Briggera*. However, careful examination of Greville's specimens showed that there was no trace of linking spines and that the species is a *Biddulphia* identical with the one described by Wise (1952: 406) as *B. sturtii* Wise, which is thus a later synonym of *B. podagrosa* Grev.

In view of the widespread occurrence of *Briggera* spp. in the upper Cretaceous and Paleogene deposits of the European part of the U.S.S.R. and western Siberia, and the presence of *B. includens* in the lower Eocene of the Isle of Fehmarn in the western Baltic, it is surprising that no undoubted member of the genus occurs in the lower Eocene deposits of Denmark, the flora of which has many similarities to that of contemporary deposits in the U.S.S.R. Material from the Danish deposits is well represented in the collections of the British Museum (Natural History) but we have found no member of the genus in these preparations. However, *Hemiaulus mirus* A. Schmidt (1889: taf. 142 fig. 33), which came from Mors, Denmark, is not represented in them and the original illustration suggests that it may be a species of *Briggera* distinct from any described here. The specimen illustrated by Schmidt has a central dome, with two not very deep sulci on either side between this and the apex, and the valve is raised as a half dome distal to the more distal of these; there are very slightly raised elevations at the apex and there is a linking spine depicted on each of these which projects proximally and is slightly curved upwards. This linking spine looks much more like a broken linking spine of a *Briggera* than the normally much more erect spine of a *Hemiaulus*. The linking spines of *Briggera includens* are depicted in a very similar way in two of Schmidt's figures on the same plate (Schmidt, 1889: taf. 142 figs 25, 27). Examination of specimens of the species is the only way in which it will be possible to decide whether *Hemiaulus mirus* should be transferred to *Briggera*, but it seems likely that this will be found to be the case.

II. ***DICLADIOPSIS*** De Toni, *Syll. Alg.* **2**: 1003 (1894).

Frustules probably all heterovalvar and joined in pairs, with one valve with interlocking linking spines and one without, rectangular, their pervalvar axis greater to much greater than their apical axis. Valves elliptical to broadly elliptical, not crossed by sulci, with two elevations arising somewhat proximal to the apices, taller on the valves without linking spines than on those with linking spines. Pseudocelli moderately large, with indefinite margins, on the distal side of the tips of the elevations, sometimes extending onto their summits. Linking spines 2–5, on the proximal side of the summits of the elevations, their bases triangular, their upper parts concave towards the centre of the valve, expanded above and interlocking. Areolae poroidal, with a raised external rim, except for those in the mantle, sparse and scattered. No labiate process seen. The only girdle elements seen valvocopulae that are open bands.

TYPE SPECIES: *Dicladiopsis barbadensis* (Grev.) De Toni, loc. cit., lectotype designated here.

De Toni (1894) recognized that *Dicladia barbadensis* Grev. and *D. robusta* Grev. were very distinct from *D. capreolus* Ehrenb., the type species of the genus, and he erected for them the genus *Dicladiopsis* which he placed in the Chaetoceraceae. Examination of the type specimens of Greville's two species showed that they are conspecific. Greville (1865*c*) described *Dicladia robusta* as having only one elevation on each valve, but its type specimen is mounted with the transapical axis in the plane of the microscope slide so that the two elevations on each valve are superimposed. Careful differential focusing shows that each valve has two elevations. As the description of *D. barbadensis* is the more accurate, and also as it was published slightly earlier than *D. robusta*, we have designated it as the lectotype of the genus. In the entry for *Dicladiopsis* De Toni in the *Index Nominum Genericorum* (Farr, Leussink & Stafleu, 1979) prepared by one of us (R.R.) it is said that *D. barbadensis* (Grev.) De Toni is the holotype of the genus but this is an error. De Toni (1894) included both *D. barbadensis* and *D. robusta* (Grev.) De Toni in the genus when establishing it without indicating which was the type and the fact that *Dicladia barbadensis* Grev. was published earlier than *Dicladia robusta* Grev. does not automatically make it the type of De Toni's genus.

In Greville's collection in the British Museum (Natural History) there are five specimens of *Dicladiopsis barbadensis* from Cambridge, Barbados, all of them complete frustules each of which is heterovalvar, one valve with linking spines and one without. Whilst it is not certain that the linking spines of this species are expanded above and interlock, the well developed pseudocelli with indefinite margins, the robust elevations with linking spines arising from the proximal side of the summits of the elevations and the small poroid areolae all indicate the relationship of this species to *Briggera*. As far as we are aware, no other specimens of *D. barbadensis* have been found.

In the upper Eocene material from the U.S.S.R. we have found specimens of four other species that we consider to be congeneric with *Dicladiopsis barbadensis*. Of one of these, *Dicladiopsis* sp. I, we found a whole frustule which is heterovalvar, one valve possessing interlocking linking spines and the other lacking them. This is the only whole frustule of any of these four species that we have found. In addition to this whole frustule we have seen only one other specimen of this species; this consists of a single valve with linking spines. All the specimens of the other species have been single valves, except for one that consists of a pair of sibling valves connected by interlocking linking spines. Of the four specimens of *D. alta* R. Ross & P. A. Sims that we have seen, one has linking spines (Pl. 17 figs 1, 5); one of the others does not have linking spines (Pl. 17 figs 2, 6) but the tips of the elevations of the other two, examined with the light microscope, are broken off and we cannot say whether or not they had linking spines. All the specimens of *D. perlonga* (Pant.) R. Ross & P. A. Sims had the tips of their elevations broken off. We have seen 19 specimens of this species of which seven had the margin of the valve broken away. Five of those with intact margins had a marginal ridge within which the valve was slightly depressed and the other seven had no marginal ridge and no depression. The two types of valve of *D. barbadensis* differ in a very similar way. There is thus a strong indication that the frustules of this species are heterovalvar. The evidence is less strong for *D. erecta* R. Ross & P. A. Sims. We have seen eleven specimens of this species with linking spines, but only three, two of which have the tops of their elevations broken off, of the sort that we believe to be valves without linking spines of this species. Whether this disproportion means that the cells occurred in chains more than two cells long or whether it is due to some bias in preservation or in selecting specimens for mounting we cannot tell.

There is considerable similarity between the valves of *Dicladiopsis* with linking spines and those of *Briggera*, in particular those of the species with elliptical valves. They differ, however, quite appreciably in the contour of the valve, in the absence of sulci and in the sparser and more irregularly placed areolae. These differences, together with the likelihood that the frustules of *Dicladiopsis* are all heterovalvar, are sufficient grounds for separating the genera.

The comparative sparseness of the areolae, particularly in *Dicladiopsis barbadensis* and *D. alta*, together with the heterovalvar frustules, give the species of this genus the appearance of spores. However, if *D. barbadensis, D. alta,* and *D. perlonga* are spores, they must have been formed in pairs in frustules with a pervalvar length of 400 μm or more; whilst this is not impossible, it seems unlikely. There are no diatoms in the deposits in which they are found that seem to be possible vegetative cells of species of which these might be spores.

This genus is apparently confined to the middle and upper Eocene and is always infrequent in the deposits in which it is found.

Key to the species

1a Valves without a vertical row of areolae on the distal side of each elevation:
  2a Height to the summit of the elevations more than twice the height to the centre of the valve ... 1. ***barbadensis***(p. 319)
  2b Height to the summit of the elevations no more than one and a half times the height to the centre of the valve .... ***Didadiopsis*** sp. I (p. 323)
1b Valves with a vertical row of areolae on the distal side of each elevation:
  3a Elevations swollen on their proximal sides a short distance above their bases .... 2. ***alta***(p. 320)
  3b Elevations not swollen above their bases:
    4a Superficial spines present .... 3. ***erecta***(p. 321)
    4b Superficial spines absent .... 4. ***perlonga***(p. 322)

1. **Dicladiopsis barbadensis** (Grev.) De Toni, *Syll. Alg.* **2**: 1003 (1894). (Pl. 32 fig. 3a, b, c)

Dicladia barbadensis Grev. in *Trans. microsc. Soc. Lond.* II, **13**: 56, pl. 6 fig. 28 (1865).
Dicladia robusta Grev., tom. cit.: 98, pl. 8 fig. 11 (1865).
Dicladiopsis robusta (Grev.) De Toni, loc. cit. (1894).

Frustules with pervalvar axis many times longer than the apical axis, heterovalvar with one valve with linking spines and the other without. Valves elliptical to sub-circular, 35–55 μm long, 42 μm broad in the one specimen seen in polar view; valves with linking spines with a vertical mantle up to 4 μm deep, valve surface not depressed within the mantle and sloping upwards to a short central column that widens slightly above to the bases of the elevations, slightly domed between these in the larger specimens, height at the centre of the valve 10–20 μm; valves without linking spines with a vertical mantle 8–10 μm deep, its upper part a marginal ridge within which the valve surface is depressed and then, towards the centre, rises in a column that expands considerably below the bases of the elevations, sometimes slightly domed between the bases of the elevations in the larger specimens, height at the centre of the valve 14–30 μm. Elevations arising from the summit of the central column, sloping slightly outwards in their lower part and rather more strongly in their upper part, tapering gradually upwards, sometimes with a slight rounded projection on their proximal sides near the base of the elevation; elevations without linking spines taller than those with linking spines on the valves of the same frustule, height to the summit of those with linking spines 30–50 μm, of those without linking spines 38–78 μm. Areolae poroid, 0·2 μm or less in diameter, in a single row 6–8 in 10 μm around each mantle and also scattered and 10–12 in 10 μm on the mantle of valves without linking spines, elsewhere very few or nil. Superficial spines present, up to 5 μm long, scattered and up to 3 in 10 μm over the whole valve surface. Pseudocelli on the distal half of the tips of the elevations, areolae *c.* 20 in 10 μm. Linking spines probably two on each elevation, *c.* 4 μm tall. Valvocopula *c.* 15 μm deep with areolae in vertical rows, rows *c.* 20 in 10 μm, areolae *c.* 17 in 10 μm.

Middle Eocene. Cambridge, Barbados (BM 3179, 3409, 3416 holotype, 3428, 3465; Greville 1865*b*, *c*).

The five specimens of this species that we have seen are all mounted in girdle view. They each consist of a whole frustule with two different valves, one with linking spines and one without, the two valves in every case abutting one to the other. One of them has a valvocopula *c.* 15 μm deep attached; the others have a single girdle band around the two valves that appears to belong to the parent frustule and not to be attached to either of the valves. The holotype of *Dicladia robusta* (BM 3179) is a specimen of this species lying with the pervalvar and transapical axes in the plane of the slide on which it is mounted, so that the two elevations of each valve are superimposed. Careful focusing makes it plain that there are two elevations on each valve, not one as shown in Greville's (1865*c*) drawing, and that this specimen is conspecific with the others.

Dicladiopsis barbadensis has very few or no areolae on the valves other than those on the mantle and those of the pseudocelli. In this respect it resembles *D. alta* R. Ross & P. A. Sims, but the other three species of the genus have many more. *D. alta* has a vertical row of areolae on the distal face of its elevations, which *D. barbadensis* does not. The only other species without this vertical row of areolae is *Dicladiopsis* sp. I, but this has much shorter and stouter elevations, larger pseudocelli and many more areolae.

All the five specimens of this species that we have seen are on slides prepared by Greville of material from Cambridge, Barbados, which is of middle Eocene date. As far as we are aware, no other specimens of this species have been found.

2. **Dicladiopsis alta** R. Ross & P. A. Sims, **sp. nov.** (Pl. 17 figs 1–8, Pl. 32 fig. 4)

Valva late elliptica, 30–50 μm longa, 22–30 μm lata, limbo verticali 7–12 μm alta; superficies valvae intra limbum depressa et intra zonam depressam columnam supra expansam elevationibus ex summo exorientibus formans; altitudo ad centrum valvae 30–43 μm. Elevationes infra verticales, supra polos versus leniter inclinatae, tumore in lateribus proximalibus suis ab basibus non procul distanti, supra eum gradatim angustatae; altitudo ad vertices elevationum 95–125 μm. Areolae poroides, diametro 0·1–0·2 μm, in superficie valvae et in elevationibus sparsim dispersae, in elevationibus seriem verticalem, 12–15 in 10 μm, in latere distali utraeque formantes, in limbo dispersae et 5–9 in 10 μm aut nullae. Spinae superficiales minimae, 1–2 in 10 μm, in elevationibus, nonnumquam absentes. Pseudocellus in latere distali et dimidio distali verticis summi utraeque elevationis, diametro 4–5 μm, areolis *c.* 30 in 10 μm. Spinae ligantes 2 in utraeque elevatione, ut videtur non supra expansae, *c.* 3 μm altae.
TYPUS: BM 65772, ex stratis eocaenicis superioribus ad 'Kamichev' (ut videtur 'Kamyshlov, Sverdlovsk oblast, U.S.S.R.').

Valve broadly elliptical, 30–50 μm long, 22–30 μm broad, with a vertical mantle 7–12 μm deep; valve surface depressed within the mantle and within the depressed zone rising in a column that expands above with the elevations arising from its summit; height at the centre of the valve 30–43 μm. Elevations vertical below and sloping slightly outwards above, with a swelling on their proximal sides not far above their bases, and gradually tapering above this swelling; height to the summit of the elevations 95–125 μm. Areolae poroid, 0·1–0·2 μm in diameter, sparsely scattered on the valve surface and the elevations, 1–3 in 10 μm, and a vertical row on the distal face of the elevations, 12–15 in 10 μm, scattered and 5–9 in 10 μm on the mantle, but none on the mantle of one specimen. Scattered very small superficial spines, 1–2 in 10 μm usually present, sometimes absent. Pseudocellus on the distal side and the distal half of the summit of the tip of each elevation, 4–5 μm in diameter, the areolae *c.* 30 in 10 μm. Linking spines two on each elevation, apparently not expanded above, *c.* 3 μm tall.

Upper Eocene. 'Kamichev', presumed to be Kamyshlov, Sverdlovsk oblast, U.S.S.R. (BM 65772, 81110, SEM CB15.354–355, CB18.438–445, 2947–2951, 2980, 4680–4689, 4691–4696, 4706–4714).

The above description is based on four specimens, all single valves with no girdle elements attached. Two of these have been examined with the scanning electron microscope, of which one has its elevations almost intact at the tip except that parts of the pseudocelli are broken away, and also all but one of the linking spines (Pl. 17 figs 1, 5); the other specimen has its pseudocelli broken away but clearly did not have linking spines (Pl. 17 figs 2, 6). The specimen with linking spines has no superficial spines (Pl. 17, fig. 1) and no areolae on its mantle (Pl. 17, fig. 3); both these are present on the one without linking spines (Pl. 17 figs 2, 4). The elevations of the one with linking spines are further apart at the base than those of the specimen without linking spines, the distance between them being *c.* 10 μm as against *c.* 5 μm. This difference in the insertion of the elevations is similar to that between the valves with and without linking spines of *Dicladiopsis barbadensis* and we therefore consider it likely that the two valves examined with the scanning electron microscope are the two types of valve of a heterovalvar species. Using this criterion, the two valves examined with the light microscope, one of them the holotype, appear to be valves with linking spines for their elevations are 10 μm and 14 μm apart at the base. The absence of superficial spines on one of the specimens does not seem to be due to erosion; it is in other ways the best preserved. It is, however, so similar to the others in all other respects that we consider this difference to be infraspecific variation.

This species is much closer to *Dicladiopsis barbadensis* than to any of the other species of the genus in its general shape and in the sparseness of the areolae, but that species does not have the very prominent bulge of the elevations slightly above their bases nor the vertical row of areolae on the distal face of the elevations; the elevations of *D. alta* are also appreciably taller than those of *D. barbadensis* and this characteristic is the reason for our choice of specific epithet. *D. alta* also resembles in general shape of valve the specimens that we consider to be the valves without linking spines of *D. erecta* R. Ross & P. A. Sims, but these have more areolae and a much deeper mantle; also they lack the prominent bulge on the elevations and the well developed column below their insertion. Whilst there is a possibility that we may have considered specimens that belong to this species as valves without linking spines of *D. erecta*, the presence of linking spines on one of the specimens of this species shows clearly that it is not conspecific with the very different specimens of *D. erecta* with linking spines, one of which is the type of the species.

3. **Dicladiopsis erecta** R. Ross & P. A. Sims, **sp. nov.** (Pl. 18 figs 1–7, Pl. 32 figs 5–7)

? *Keratophora robusta* sensu Jousé in Proshkina-Lavrenko et al., *Diat. Anal* **2**: 205, pro parte, quoad tabl. 77 fig. 3b (1949), non Pantocsek.

Valva elliptica ad late elliptica, 25–85 μm longa, 22–60 μm lata. Valva spinis ligantibus instructa limbo verticali 6–11 μm alto; superficies valvae intra limbo paullo depressa et intra zonam depressam ad bases elevationum et tholum centralem errigens; altitudo ad centrum valvae 15–28 μm; elevationes apicibus proximaliter exorientes, erectae, vel quae infra polos versus leniter inclinatae sunt et supra gradatim verticales fiunt, summis lateraliter paullo et distaliter inflatis; altitudo ad vertices elevationum 35–55 μm; areolae poroides, extrinsecus margine elevato, diametro 0·3–0·5 μm, in superficie valvae et in lateribus proximalibus sed non distalibus elevationum inordinate et sparsim dispersae, 2–6 in 10 μm, in limbo crebriores, 8–10 in 10 μm, et sine marginibus elevatis; series verticalis areolarum aliquantum inordinata in latere distali utraeque elevationis, 12–15 in 10 μm; spinae superficiales usque ad 5 μm longae, saepe ex margine elevato areolae exorientes, in superfice valvae et parte inferiore proximali elevationum dispersae, 2–4 in 10 μm; pseudocelli in partibus distalibus summorum elevationum, areolis in seriebus inordinate dispositis et curtis, *c.* 25 in 10 μm, et areolis paucis in verticibus elevationum; spinae ligantes 4–5, in semi-circulo in latere proximali verticis utraeque elevationis dispositae, supra expansae, in latere proximali concavae, *c.* 10 μm altae. Valva sine spinis ligantibus limbo altiore, *c.* 15 μm alta; superficies valvae intra limbum paullo depressa; valva, aspectu cingulari, intra zonam depressam aliquantum contracta et supra expansa et portionem tholiformem, elevationibus ex partibus apicalibus ejus exorientibus, faciens; altitudo ad centrum valvae 30–40 μm; elevationes altior quam eae valvarum spinis ligantibus instructis; altitudo ad vertices elevationum 70–90 μm; areolae in serie verticali distali in utraque elevatione sparsiores, 2–4 in 10 μm; alibi ut valva spinis ligantibus instructa.
TYPUS: BM coll. Adams TS747, ex stratis eocaenicis superioribus ad 'Kamichev' (ut videtur 'Kamyshlov, Sverdlovsk oblast, U.S.S.R').

Valve elliptical to broadly elliptical, 25–85 μm long, 22–60 μm broad. Valve with linking spines with a vertical mantle 6–11 μm deep, slightly depressed within this and then rising to the bases of the elevations and a central dome; height at the centre of the valve 15–28 μm; elevations arising proximal to the apices, erect or slightly inclined outwards in the lower part and curving gradually to vertical above, at the tips swollen distally and slightly laterally; height to the summit of the elevations 35–55 μm; areolae poroid, with a raised external rim, 0·3–0·5 μm in diameter, irregularly and sparsely scattered over the valve surface and the proximal but not the distal sides of the elevations, 2–6 in 10 μm, closer together, 8–10 in 10 μm, and without external rims on the valve mantle; a somewhat irregular vertical row of areolae 12–15 in 10 μm on the distal face of each elevation; scattered superficial spines up to 5 μm long on the valve surface and the lower proximal part of the elevations, often arising from the raised rim of an areola, 2–4 in 10 μm; pseudocelli on the distal part of the tips of the elevations, their areolae in irregularly arranged short rows, *c.* 25 in 10 μm, and a few areolae on the summit of the elevations; linking spines 4–5 on each elevation, inserted in a semi-circle on the proximal side of the summit of the elevation, expanded above, concave on the proximal side, *c.* 10 μm tall. Valve without linking spines with a deeper mantle, 15 μm deep; valve surface slightly depressed immediately within this, in girdle view slightly constricted within the depressed portion and expanding above to a domed portion from the apical parts of which the elevations arise; height to the centre of the valve 30–40 μm; elevations taller than those of valves with linking spines; height to the summits of the elevations 70–90 μm; the vertical row of areolae on the distal sides of the elevations sparser than on those with linking spines, 2–4 in 10 μm; otherwise as valves with linking spines.

Upper Eocene. 'Kamichev', presumed to be Kamyshlov, Sverdlovsk oblast, U.S.S.R. (BM 65797, 65808, 81111, coll. Adams TS 747, SEM CB15.352–353, CB15.356–357, CB18.457–464, CB18.471–481, 2935–2946, 2955–2959, 2979, 2981–2983, 4099–4105, 4690, 4703–4705).

? Staroverovka, Voroshilovgrad oblast, U.S.S.R. (Jousé in Proshkina-Lavrenko et al., 1949*b*; Glezer, Zosimovich & Klyushnikov, 1965).

All the specimens of this species that we have seen have had no girdle elements attached to them and all have been single valves except for the holotype, which consists of a pair of sibling valves united by their interlocking linking spines. We have thus no firm evidence that the two types of valve that we have associated together do in fact belong to the same species. However, the fact that they differ from one another in the same way as the two types of valve of *Dicladiopsis barbadensis* and *Dicladiopsis* sp. I but otherwise resemble each other so closely seems to us adequate ground for considering them to be the two types of valve of one species. Because of this slight uncertainty we have dealt with the two types of valve separately in the description of the species.

As we have already pointed out (p. 318), we have seen many more specimens of this species with linking spines than we have of the type that we consider to be the valves without linking spines, and there is thus a possibility that there were more than two cells in a chain of this species and not all its frustules were heterovalvar.

The differences between this species and *Dicladiopsis alta* have been discussed under that species (p. 321). *D. erecta* differs from *D. perlonga* (Pant.) R. Ross & P. A. Sims, which also has a vertical row of areolae on the distal face of the elevations, by the possession of superficial spines, by the invariable presence of a vertical mantle sharply delimited from the valve surface, and by the sparser areolae; also, in *D. perlonga* the lower parts of the elevations are very oblique, whereas in *D. erecta*, even in the valves without linking spines, they are almost vertical throughout. It is to this feature that the specific epithet chosen refers. In *Dicladiopsis* sp. I also the elevations have oblique lower parts, and there is no vertical row of areolae on the distal face of the elevations, which are less tall than those of *D. erecta*.

All the specimens that we have seen come from the material labelled 'Kamichev', which we believe to have come from the upper Eocene deposit at Kamyshlov, Sverdlovsk oblast, U.S.S.R. (see p. 280 above). As we point out below (p. 323), one of the two specimens illustrated by Jousé under the name *Keratophora robusta*, that from Staroverovka, Voroshilovgrad oblast, U.S.S.R. (Jousé in Proshkina-Lavrenko et al., 1949*b*: tabl. 77 fig. 3b) is probably *Dicladiopsis erecta*, although the figure is not good enough for us to be certain.

4. **Dicladiopsis perlonga** (Pant.) R. Ross & P. A. Sims, **comb. nov.** (Pl. 32 figs 8–9)

Hemiaulus perlongus Pant., *Beitr. Kenntn. Foss. Bacill. Ungarns* **2**: 82, taf. 20 fig. 315 (1889); Laporte & Lefébure, *Diat. rares et cur.* **2**: pl. 21 fig. 148 (1930).

? *Keratophora robusta* sensu Jousé in Proshkina-Lavrenko et al., *Diat. Anal.* **2**: 205, tabl. 77 fig. 3a (1949), excl. fig. 3b, non Pantocsek.

Valves broadly elliptical, 55–140 μm long, 40–95 μm broad, some valves with a vertical mantle continuous with a marginal ridge, the two together 8–9 μm deep, others with no marginal ridge and a vertical mantle 0–4 μm deep, the valve surface rising gently from the mantle or a slight depression within the marginal ridge to a raised central portion from which the elevations arise; between the bases of the elevations a very small dome usually present; height to the centre of the valve 21–35 μm. Elevations arising from the central raised part of the valve, their lower parts strongly inclined outwards and curving to become vertical above, the tips broken off in every specimen seen; height to the summit of the elevations 65–120 μm. Areolae poroid, 0·5–1·0 μm in diameter, scattered and 2–4 in 10 μm on the valve surface but sometimes sparser near the centre, very few or absent on the elevations except for a vertical line on their distal face, 4–6 in 10 μm, none on the mantle. No superficial spines. Pseudocelli present on the tips of the elevations but not more than their lower margins present on any specimen seen. No linking spines seen. No labiate process seen.

Upper Eocene. Kuznetsk, Penza oblast, U.S.S.R. (BM 64045, 74799, 75045, 75050, coll. Adams J334, J2668, TS441; Pantocsek, 1889; Laporte & Lefébure, 1930).
Rostov, U.S.S.R. (for this locality see p. 281) (BM 81112, 81113).
Voronezh oblast, U.S.S.R. (Jousé in Proshkina-Lavrenko et al., 1949*b*).

All the 19 specimens of this species that we have seen have been single valves with the tips of the elevations broken off, and Pantocsek's (1889) illustration of the type specimen shows that this was in the same state. In many cases this break occurs at the lower edge of the pseudocellus at the position of its outermost areolae and this enables us to know that one was present, although we can give no details of it. We also cannot be certain that linking spines are present in this species. All the specimens seem to be somewhat eroded and the areolae of many have probably been enlarged; the maximum figure that we give for their diameter is thus probably appreciably greater than their size when the diatom was alive. Many of the specimens, too, have the margins broken away. Of those where the margin is certainly present five have a marginal ridge and seven do not. The specimens with a marginal ridge when seen in girdle view have the valve slightly constricted below the base of the elevations whilst those without marginal ridge do not have this constriction, but there are no other differences. The two types of valve thus differ in the same way as the two types of valve of *Dicladiopsis barbadensis* and *Dicladiopsis* sp. I and the proportion of each type strongly suggests that the frustules were normally heterovalvar, as in those species. This, added to their general similarity to *D. barbadensis* in particular, is good reason for transferring the species to *Dicladiopsis*. It is clearly misplaced in *Hemiaulus* Heib.

Jousé (in Proshkina-Lavrenko et al., 1949*b*: 205) treats *Hemiaulus perlongus* Pant. as a synonym of *Keratophora robusta* Pant., the type of which is not a diatom. She accompanies her account of this species with two figures which are too crude for certain identification and her description of *K. robusta* is so sketchy that it gives no further useful information. However, one of her figures (tabl. 77 fig. 3a), of a specimen from Voronezh oblast, is more likely to be of *Dicladiopsis perlonga* than of any other species. The age she gives for this specimen is Paleocene but according to Glezer (in Glezer et al., 1974: 130–133) the material from Voronezh oblast is of upper Eocene age. Jousé's other figure (tabl. 77 fig. 3b) is of a specimen with superficial spines and elevations that are much less oblique at the base, and this we think is more probably *D. erecta*. The specimen came from Staroverovka in Voroshilovgrad oblast, U.S.S.R. Glezer, Zosimovich & Klyushnikov (1965) record *Hemiaulus perlongus* and *Keratophora robusta* as separate species from upper Eocene deposits in Voroshilovgrad oblast, pointing out at the same time that this, and not Oligocene as stated by Jousé, is the age of this material. The fact that they recognized these two species in these deposits suggests that two species of *Dicladiopsis* occur there, although their records may be based on the two types of valve of one heterovalvar species. Jousé's fig. 3b suggests that one of these is *D. erecta* but, in the absence of any illustrations, the identity of the other is uncertain.

In addition, Glezer & Sheshukova-Poretskaya (1969) record *Hemiaulus perlongus* from upper Eocene material from Chernigov oblast, Ukraine, U.S.S.R., and Glezer (in Glezer et al., 1974) records it in material of the same age from Kazakhstan. These records are almost certainly based on species of *Dicladiopsis* but as they too are not accompanied by illustrations it is impossible to say which. We have accordingly not included them in the distributions of any of the species.

Dicladiopsis sp. I (Pl. 19 figs 1–7)

Frustule with the pervalvar axis much exceeding the apical axis. Valve elliptical to broadly elliptical, 40–100 μm long, 25–68 μm broad, with a vertical mantle 5–9 μm deep, with a poorly developed marginal ridge; surface of the valve slightly depressed within the margin and with the central part domed; height to the centre of valve with linking spines 26–35 μm, of valve without linking spines (the only one seen) 32 μm. Elevations arising immediately distal to the domed central part of the valve, inclined outwards, but those with linking spines abruptly becoming vertical and with tips laterally expanded and flattened above; those without linking spines inclined outwards throughout, with their tips rounded above and not expanded; height to the summit of elevations with linking spines 31–43 μm, of those without linking spines 45 μm. Areolae circular to narrowly elliptical, with a raised external rim, except for those on the mantle, diameter *c.* 0·2 μm to 0·8 × 0·2 μm, sparsely and irregularly scattered over the whole valve surface including the elevations, 2–4 in 10 μm, denser and 6–8 in 10 μm on the mantle. Scattered superficial spines up to 5 μm long, often arising from the raised rim of the areolae, on the valve surface and the lower parts of the elevations, 2–3 in 10 μm. Pseudocellus on the distal half of the tip of each elevation and, in those without linking spines, on the summit, 6–15 μm in diameter, their areolae irregularly arranged and 20–22 in 10 μm. Linking spines 2–3 on each elevation, on the proximal side of the summit, up to 5 μm long, not much expanded above. Valvocopula an open band *c.* 15 μm deep, with areolae in interrupted vertical rows, rows *c.* 27 in 10 μm, areolae 12–18 in 10 μm but closer near the abvalvar margins.

Upper Eocene. 'Kamichev', presumed to be Kamyshlov, Sverdlovsk oblast, U.S.S.R. (BM SEM B17.684–685, B17.891–902, B27.532–539, CB16.496–514, CB16.775–776, 1943–1959).

We have examined two specimens of this species with the scanning electron microscope, but have not been able to find another that we could mount for light microscopy and designate as a holotype. For this reason we do not publish a name for this species. One of the specimens we have seen is a single valve, the other (Pl. 19) is a whole frustule with the valvocopula attached to the epivalve. The two valves of this frustule are in contact and it is thus presumably at the stage shortly after cell division. Although no pairs of sibling valves joined by their linking spines have been found, one intact linking spine and also the grooves on the proximal sides of the tips of the elevations show that the linking spines narrow gradually for some distance above their bases and then widen. In this they differ from those of *D. erecta* and of *Briggera*, where the spines are narrowest close to their bases.

These specimens have elevations wider relative to their height than those of any other species of *Dicladiopsis*. They resemble *D. erecta* more closely than any of the other species of the genus; the general shape of the valve and the distribution of the areolae is very alike and both have similar superficial spines. However, *Dicladiopsis* sp. I has oblique, not almost erect, elevations and larger pseudocelli and it lacks the vertical row of areolae on the distal face of the elevations.

Dicladiopsis sp. I is apparently considerably rarer in the material from 'Kamichev' than *D. erecta* and we have found it nowhere else. Whether any of the published records of *Hemiaulus perlongus* Pant. or *Keratophora robusta* Pant. discussed under *D. perlonga* (Pant.) R. Ross & P. A. Sims (p. 323) are based on this species cannot be decided at present, but it is possible that one or more of them is.

III. ***STRELNIKOVIA*** R. Ross & P. A. Sims, **gen. nov.**

Frustula in catenis rectis inseparabilis conjuncta. Valvae bipolares, elevationibus duabus magnis sed, in speciebus nonnullis, parum elevatis, ad vel prope apices exorientibus. Areolae poroides, parvae, in seriebus interruptis radialibus dispositae vel sparsae et inordinate dispersae. Pseudocelli magni, in parte distali elevationum, nonnumquam in limbum, nonnumquam in verticem elevationum extendentes, areolis ad margines sparsioribus. Spinae ligantes implexae, 12 minimum, saepe plures, ad marginales proximales et laterales verticum elevationum, vel eos, praeter partem minimum distalem, cingentes, basibus suis linearibus vel anguste ellipticis, a centro elevationum radiatis, partibus superioribus suis latioribus, aspectu laterali triangulares. Rimoportulae nonnumquam una vel duae prope marginem in portione centrali valvae, nonnumquam 6–8 circum aream centralem, aperturis interioribus suis rectis et parum elevatis; in speciebus aliquis nullae visae. Cingulum maturum ex tribus minimum taeniis apertis, seriebus verticalibus areolarum poroidum nonnumquam interruptis ornatis, constans.
SPECIES TYPICA: *Strelnikovia antiqua* (Streln.) R. Ross & P. A. Sims, comb. nov., infra (p. 326).

Frustules united in straight inseparable chains. Valves bipolar, with large but, in some species, not much raised elevations arising at or near the apices. Areolae poroid, small, in interrupted radial rows or sparse and scattered. Large pseudocelli on the distal part of the elevations, sometimes extending onto the mantle, sometimes onto the summits of the elevations, their areolae sparser at the margins. Linking spines interlocking, at least 12 in number, often many more, on the proximal and lateral margins of the summits of elevations or surrounding these except for a small gap on the distal side, their bases linear or narrowly elliptical, radiating from the centre of the elevations, their upper parts wider, triangular in side view. Labiate processes sometimes one or two near the margin in the central portion of the valve, sometimes 6–8 in a ring around the central area, their inner openings straight and slightly raised; in some species none seen. Mature cingulum of at least three elements open at one end, with vertical rows of poroid areolae sometimes interrupted by hyaline bands.

When describing *Rutilaria antiqua* as a new species, Strel'nikova (1964) expressed the view that it might not be a species of *Rutilaria* but instead represent an undescribed genus. It, and the other species included here in *Strelnikovia*, are not at all closely related to *Rutilaria*, which has a central labiate process modified to form a linking structure quite different from the interlocking linking spines of *Strelnikovia* and its allies. Also, *Rutilaria* has at its apices ocelli of the type found in the Eupodiscaceae, which would indicate that its affinities are with that family and not with the Biddulphiaceae, to which *Strelnikovia* belongs, as its pseudocelli with indefinite margins show.

The elevations of *Strelnikovia* are both stouter and in some species shorter than those of any of the other genera with interlocking linking spines and large pseudocelli. From *Briggera*, some species of which most closely approach it in this respect, it differs in the much greater number of its linking spines and their narrower bases. The linking spines of *Dicladiopsis* are similar in number and shape to those of *Briggera*, and *Dicladiopsis* has much taller and narrower elevations than any found in *Strelnikovia*; it, too, apparently has all its frustules heterovalvar. The other two genera with many narrow linking spines, *Keratophora* Pant. and *Thaumatonema* Grev., have a complete ring of linking spines around the summit of their elevations, whereas in *Strelnikovia* the ring is always incomplete with a distal gap, which may, however, be very small. In both *Keratophora* and *Thaumatonema* the elevations are much less stout than those in *Strelnikovia* and are inserted much closer to the centre of the valve.

Six species of this genus, possibly seven (see p. 328), have been found in the Campanian (upper Cretaceous) deposits from the eastern slopes of the northern Ural mountains but from nowhere else. In addition, there is a species, *Strelnikovia incerta* R. Ross & P. A. Sims, that we have assigned, with some hesitation, to this genus; it comes from 'Kamichev', material which we believe comes from the upper Eocene deposit at Kamyshlov, Sverdlovsk oblast, U.S.S.R. (see p. 280). It would seem therefore, if our suppositions about the generic position and the provenance of this species are correct, that the genus persisted from the Campanian to the upper Eocene, although it may have been confined to the Campanian. Our knowledge of the diatom floras of the world during the relevant period is too scanty for us to conclude from its known distribution that it was in fact confined to the limited area on the eastern side of the Ural mountains from which all the known specimens have come. It is somewhat surprising, however, that no specimens have been found in deposits from elsewhere laid down during the period in which it was apparently present there.

Key to the species

1a Elevations at least twice as long as wide, usually narrowing towards the centre of the valve:
2a Valve without transverse sulci, with an obvious marginal ridge .... 1. ***antiqua*** (p. 326)
2b Valve with two transverse sulci, without a marginal ridge .... 6. ***incerta*** (p. 331)
1b Elevations little, if any, longer than wide, circular in cross section or narrowing towards the apices of the valve:
3a Areolae in interrupted radial rows:
4a Valve with a marginal ridge:
5a Elevations with a swelling on their distal sides, total height *c.* 20 μm......... 2. ***tumida*** (p. 327)
5b Elevations without a swelling on their distal sides, total height *c.* 50 μm .... 3. ***auliscoformis*** (p. 328)
4b Valve without a marginal ridge:
6a Linking spines confined to the proximal half of the circular summit of the elevations 4. ***inclinata*** (p. 329)
6b Linking spines surrounding the kidney-shaped summit of the elevations except for a very small distal gap .... 5. ***reniformis*** (p. 330)
3b Areolae sparse and scattered.. ***Strelnikovia* sp. I** (p. 332)

1. **Strelnikovia antiqua** (Streln.) R. Ross & P. A. Sims, **comb. nov.** (Pl. 20 figs 1–6, Pl. 21 figs 1–7, Pl. 33 fig. 1)

Rutilaria antiqua Streln. in *Trudy vses. neft. nauchno-issled. geol.-razv. Inst.* **239**: 230, tabl. 2 (p. 475) fig. 1 a–e (1964), *Diat. pozdn. Mela* (*Zap. Sibir'*): 109, t. 53 figs 1–3 (1974).

Frustule with the pervalvar axis about half as long as the apical axis. Valve subrhombic with slightly tapering projections not sharply delimited from the central portion of the valve and rounded at the apices; valves 80–170 μm long, 30–55 μm broad, with a mantle *c.* 6 μm deep, vertical except for a narrow concave strip immediately below the marginal ridge, interrupted, like that, around the apices of the valve. Valve surface slightly raised in the centre, elsewhere, except for the elevations, flat. Elevations large, not much raised, elongated along the apical axis, narrowing towards their rounded proximal ends, height to the top of the elevations *c.* 12 μm, elevations 12–18 μm long, 5–7 μm broad. A hyaline marginal ridge, interrupted around the apices of the valve, sometimes extended upwards as a thin flange *c.* 3 μm tall on the proximal part of the projections. Areolae poroid, with raised rims on the outer surface of the valve, in interrupted radial rows, rows 12–18 in 10 μm, areolae 15–20 in 10 μm, except near the centre of the valve where they are scattered and more distant; areolae on the mantle in vertical rows, spacing as on the valve surface. A number of hollow spines or occluded processes in the centre part of the valve, sometimes few and scattered, sometimes forming a ring 10–12 μm in diameter with the spines or processes 2–3 μm apart and with a few additional ones within the ring. A row of similar spines or processes 1–3 μm apart close to the margin in the central part of the valve, from 1–2 up to *c.* 20 on each side of the valve. Pseudocelli covering the central part of the summit of the elevations and extending onto the apical part of the mantle, the areolae in curved rows converging on the centre line of the elevation, rows and areolae *c.* 30 in 10 μm. Linking spines around all but the apical end of the summit of the elevations, their bases narrowly elliptical and *c.* 0·6 μm wide, their upper parts somewhat curved inward and slightly concave on the outer side, 1·0–2·0 μm wide, those at the proximal end of the elevation the widest. One or two labiate processes present on the central part of the valve near one margin or one close to each margin, their internal opening straight and somewhat raised. Mature cingulum of at least four open bands, the gaps between the bands at alternate poles of the frustule, all bands with vertical rows of areolae, rows and areolae *c.* 22 in 10 μm.

Upper Cretaceous — Campanian. Exposure XI (14), near Til'tim, basin of the river Synya, Tyumen'sk oblast, U.S.S.R. (BM 81114; Strel'nikova 1964, 1974).

Core 82, near Ust'-Man'ya, basin of the river Severnaya Sos'va, Tyumen'sk oblast, U.S.S.R. (BM 81115, 81116, 81117, SEM CB04.541-553, CB05.454-460, CB05.462-467, CB06.975–983, CB06.986–992, CB15.076–084, CB16.644–661, 3202–3231, 3266–3276; Strel'nikova 1974). Cores 19, 22, same locality (Strel'nikova 1974).

The girdle band running across the centre of plate 21 fig. 4 is probably the pleura. It is much eroded but it appears that it had on its abvalvar part vertical rows of areolae that were much smaller and closer than those elsewhere on the girdle, the rows *c.* 40 in 10 μm, the areolae *c.* 100 in 10 μm.

In fossil material of the age from which this species comes it is impossible to be certain whether the structures shown in Pl. 21, fig. 1 are hollow spines with the tips broken off or occluded processes open at the tips when the diatom was alive. In one specimen, which showed more evidence of erosion than any other, these spines or occluded processes appear as pores through the valve, which suggests that their internal membrane is thinner than the rest of the valve. It is impossible to identify the outer opening of the labiate processes in any of our pictures and it is perhaps reasonable to assume that these cannot be distinguished from the spines or processes.

This species is the largest of the genus and is the only one in which the valve outline has projections towards the apices rather than being broadly to narrowly elliptical. The large superficial spines or occluded processes in the central part of the valve are also found in this species only.

This species occurs both in exposure XI(14) from near Til'tim in the basin of the river Synya, this being the locality from which the holotype comes, and also from several of the samples from well cores from near Ust'-Man'ya in the basin of the river Severnaya Sos'va (Strel'nikova 1964, 1965, 1974). We have seen it from both localities. It is apparently the commonest member of the genus in the Campanian material from the eastern slope of the Ural mountains.

2. **Strelnikovia tumida** R. Ross & P. A. Sims, **sp. nov.** (Pl. 22 figs 1–7, Pl. 33 fig. 2)

Rutilaria sp., Strel'nikova, *Diat. pozdn. Mela* (*Zap. Sibir'*): 109, 53 fig. 4 a–g (1974).

Valva late lanceolata, 45–100 μm longa, 30–65 μm lata, limbo parte inferiore verticali et *c.* 10 μm alta, parte superiore, praeter ad apices, profunde concava; superficies valvae concava, media in valva parum elevata. Elevationes robustae, verticales, sursum decrescentes, aspectu valvari circulares, praeter tumorem in latere distali apicem valvae attingentem; altitudo ad vertices elevationum *c.* 20 μm, diameter elevationum ad vertices *c.* 20 μm. Costa marginalis crassa, hyalina, in tota valva praeter ad apices. Area centralis hyalina diametro *c.* 2 μm, depressione *c.* 0·75 μm lata, in qua areolae nonullae adsunt, partim cincta. Areolae poroides, extrinsecus margine elevato, margine paucarum areolarum multo promentiore quam illo aliarum, in superficie valvae in seriebus radialibus magnopere interruptis dispositae, seriebus et areolis *c.* 16 in 10 μm, in verticibus elevationum inordinate dispersae, in parte verticali limbi in seriebus verticalibus dispositae, seriebus et areolis *c.* 20 in 10 μm. 2–3 spinae cavae vel processus occlusi utrinque juxta elevationes e valva exorientes. Pseudocelli in tumoribus distalibus elevationum et in limbo ad apices, seriebus areolarum a linea in axe apicali radiatis, seriebus *c.* 24 in 10 μm, areolis 26–30 in 10 μm. Spinae ligantes vertices elevationum, praeter latus distali, cingentes, partibus superioribus *c.* 1 μm latis, basibus linearibus *c.* 0·3 μm latis. Rimoportula nulla visa.
TYPUS: BM 81118, ex stratis cretaceis superioribus ad 'Ust'-Manya, Tyumen'sk oblast', Siberia.

Valves broadly lanceolate, 45–100 μm long, 30–65 μm broad, with a mantle with a vertical lower part *c.* 10 μm tall and above that deeply concave, except at the apices; valve surface concave, slightly raised at the centre. Elevations stout, vertical, tapering upwards, circular in cross section except for a swelling on their distal side that reaches to the apex of the valve; height to the top of the elevations *c.* 20 μm, diameter at the summit *c.* 20 μm. A thick hyaline marginal ridge interrupted at the apices. A central hyaline area *c.* 2 μm in diameter partially surrounded by a depression *c.* 0·75 μm broad in which some areolae are present. Areolae poroid, surrounded by a raised rim on the outer surface of the valve, this rim considerably more prominent on occasional areolae, on the surface of the valve in very interrupted radial rows, rows and areolae *c.* 16 in 10 μm, on the summits of the elevations scattered, on the vertical part of the mantle in vertical rows, rows and areolae *c.* 20 in 10 μm. 2–3 hollow spines or occluded processes arising from the valve surface on either side of each elevation. Pseudocelli on the distal swelling of the elevation and on the mantle at the apex, rows of areolae radiating from a line in the apical axis, rows *c.* 24 in 10 μm, areolae 26–30 in 10 μm. Linking spines around the summit of the elevations except for a gap on the distal side, *c.* 1 μm wide in their upper parts, *c.* 0·3 μm wide at their linear bases. No labiate process seen.

Upper Cretaceous — Campanian. Core 82 near Ust'-Man'ya, basin of the river Severnaya Sos'va, Tyumen'sk oblast, U.S.S.R. (BM 81118, SEM CB15.085–093, CB15.113, CB15.115, CB16.662–664, CB16.667–671, 2330–2352, 2464–2481; Strel'nikova 1974).

The specific epithet that we have chosen for this species refers to the swelling on the distal side of the elevation.

We have seen only two specimens of this species, the holotype and the one that we have studied under the scanning electron microscope. Both consist of a single valve and are nearly twice the size of those illustrated by Strel'nikova (1974: tabl. 53 fig. 4 a–g) under the name *Rutilaria* sp. Many of the details that distinguish the species cannot be seen on her figures and are not mentioned in her description. However, her figures 4v and 4g show that the elevations are less than 10 μm taller than the centre of the valve, and her figure 4a shows on the lower elevation the characteristic swelling on the distal side and also gives an indication of the deep concavity on the upper part of the mantle. We are thus confident that our specimen and those illustrated by Strel'nikova are the same species. The depression surrounding the central area in this species (Pl. 22 fig. 7) is a very unusual feature. It is present on both the specimens that we have seen, but cannot be seen on either of Strel'nikova's figures showing the valve view (Strel'nikova, 1974: tabl. 53 fig. 4a, b) as the centre of the valve is not in focus.

This species is much rarer than *Strelnikovia antiqua* in the Campanian material from the eastern slope of the Ural mountains. Strel'nikova (1974) recorded it from only one of the many samples from near Ust'-Man'ya that she examined, and the two specimens that we have seen also come from that locality. It has not been found in the material from the exposure near Til'tim.

3. **Strelnikovia auliscoformis** (Streln.) R. Ross & P. A. Sims, **comb. nov.** (Pl. 23 figs 1–7)

Biddulphia auliscoformis Streln. in *Trudy vses. neft. nauchno-issled. geol.-razv. Inst.* **239**: 229, t. 1 (p. 473) fig. 1 a–d (1964), *Diat. pozdn. Mela* (*Zap. Sibir'*): 93, t. 39 fig. 6, excl. figs 3–5 (1974).

Valve broadly elliptical, 70–85 μm long, 55–70 μm broad, with a vertical mantle *c.* 12 μm deep, becoming somewhat deeper at the apices; valve surface concave within the marginal ridge and rising to a ridge joining the two elevations, height to the centre of the valve *c.* 25 μm. Elevations stout, vertical, arising a little proximal to the apices, sub-triangular in section, height to the top of the elevations 40–50 μm, diameter of the elevations 15–18 μm. A hyaline marginal ridge surrounding the whole valve. A small hyaline circular central area *c.* 7·5 μm in diameter. Areolae with a raised rim on the outer surface of the valve, in slightly sinuous interrupted radial rows continuing onto the elevations, rows 15–18 in 10 μm, areolae 18–24 in 10 μm, closer near the margin than at the centre; areolae on the mantle in vertical rows, spacing as on the valve surface; occasional areolae on the valve and the elevations with higher rims than the others. Pseudocelli covering the distal half of the upper part of the elevations and their summits, the areolae in rows radiating from a transapical line in the centre of the pseudocellus, rows and areolae *c.* 30 in 10 μm. Linking spines around the proximal half of the summit of the elevations, 1·5–2 μm wide in their upper parts, *c.* 0·7 μm wide at their linear bases, triangular in side view. No labiate process seen.

Upper Cretaceous — Campanian. Exposure XI (14), near Til'tim, basin of the river Synya, Tyumen'sk oblast, U.S.S.R. (BM SEM CB15.098–101, CB15.103–104, CB15.106, CB15.108–111, CB16.672–673, CB16.677–683, 2357–2372, 2482–2492; Strel'nikova 1964, 1974).

Core 82, near Ust'Manya, basin of the river Severnaya Sos'va, Tyumensk oblast, U.S.S.R. (BM 81119; Strel'nikova, 1974).

Whilst we are confident that the diatom we have described and figured here is the one for which Strel'nikova published the name *Biddulphia auliscoformis* in 1964, we are equally confident that the specimens illustrated by her as tabl. 39 figs 3–5 of her 1974 work are a different species. These specimens have smaller elevations that are apparently circular in cross section, not sub-triangular, that are inserted further from the apices and that are inclined outwards; also they have no marginal ridge, and the specimen shown in tabl. 39 fig. 3 appears to have a central rosette of large areolae rather than a central hyaline space. There is some indication of the eroded bases of linking spines on the left-hand elevation of tabl. 39 fig. 3, and that figure thus probably represents a species of *Strelnikovia*. The central rosette is the only feature that is inconsistent with its assignment to the species described below as *S. inclinata* and that apparent feature may be spurious, the result of extraneous matter adhering to the valve. On the other hand, the diatom shown in tabl. 39 fig. 4a, b, has rounded tips to its elevations, and in that shown in fig. 5 there is no sign of linking spines on the one elevation shown in the picture; either of these two diatoms may thus belong to one of the species without linking spines, and thus not *Strelnikovia* spp., discussed above (p. 289).

The legend of tabl. 39 figs 3–6 in Strel'nikova (1974) states that all the specimens illustrated in these figures came from the river Severnaya Sos'va, but fig. 6 is identical with tabl. 1 fig. 1a in her earlier paper (Strel'nikova, 1964), which is of the holotype from Til'tim in the basin of the river Synya. Although all her other figures are of specimens that do not belong to this species, we have seen a specimen from core 82 from near Ust'Man'ya in the basin of the river Severnaya Sos'va. Strel'nikova (1974) recorded it from a number of samples from there, from cores 22, 82, and 19, but it is impossible to know how many of these records are based on the species illustrated in tabl. 39 figs 3–5 of her 1974 work and misidentified by her as *Biddulphia auliscoformis*.

There are manifest errors in dimensions in Strel'nikova's (1974) account of this species. The length is given as 17–20 μm and the breadth as 14–120 μm. Also the magnification of tabl. 39 fig. 6 is said to be × 300, although the figure is the same size as tabl. 1 fig. 1a in her 1964 paper, the identical illustration said there to be reproduced at × 600; the latter magnification agrees with the dimensions given in the 1964 paper; length 85 μm, breadth 70 μm.

4. **Strelnikovia inclinata** R. Ross & P. A. Sims, **sp. nov.** (Pl. 24 figs 1–7, Pl. 33 fig. 3)

?*Biddulphia auliscoformis* sensu Strel'nikova, *Diat. pozdn. Mela* (*Zap. Sibir'*): 93 (1974) pro parte, quoad t. 39 fig. 3, non *B. auliscoformis* Streln. (1964).

Valva late elliptica, 75–90 μm longa, *c.* 55 μm lata, limbo verticali *c.* 6 μm alta; superficies valvae ad jugum rotundatum non valde elevatum inter elevationes leniter erigens; valva ad centrum *c.* 20 μm alta. Elevationes crassae, apicibus aliquantum proximaliter exorientes, extrorsus inclinatae, aspectu valvari circulares; altitudo ad vertices elevationum *c.* 40 μm, diameter earum *c.* 17 μm. Costa marginalis nulla sed area hyalina linearis inter limbum et superficiem valvae in utroque latere valvae ab altera elevatione ad alteram. Area centralis hyalina diametro 8–10 μm. Areolae poroides, in superficie valvae et lateribus proximalibus elevationum in seriebus radialibus parum sinuatis, interruptis, in limbo in seriebus verticalibus non interruptis, dispositae, seriebus 16–17 in 10 μm, areolis *c.* 20 in 10 μm, alibi in elevationibus dispersae et sparsiores. Spinae superficiales parvae in superficie valvae dispersae, inter se 3–5 μm. Pseudocelli dimidium distalem partium superiorum et vertices elevationum tegentes, areolis suis in seriebus radiantibus, seriebus et areolis *c.* 35 in 10 μm. Spinae ligantes in dimidio proximali verticum elevationum, basibus linearibus. Rimoportula non visa.
TYPUS: BM 81120, ex stratis cretaceis ad 'Til'tim, Tyumen'sk oblast,' Siberia.

Valve broadly elliptical, 75–90 μm long, *c.* 55 μm broad, with a vertical mantle *c.* 6 μm deep, the valve surface rising gently to a not very strongly elevated rounded ridge joining the two elevations, height at the centre of the valve *c.* 20 μm. Elevations stout, arising somewhat proximal to the apices of the valve and inclined towards these, circular in cross section; height to the top of the elevations *c.* 40 μm, diameter of the elevations *c.* 17 μm. No marginal ridge but a linear hyaline area separating the valve surface from the mantle on either side between the elevations. A hyaline central area 8–10 μm in diameter. Areolae poroid, in slightly sinuous interrupted radial rows on the surface of the valve and the proximal side of the elevations, rows 16–17 in 10 μm, areolae *c.* 20 in 10 μm, scattered and sparser on the lateral and distal parts of the elevations, in uninterrupted vertical rows on the mantle, spacing as on the valve surface. Scattered small superficial spines on the valve surface, 3–5 μm apart. Pseudocelli covering the distal half of the upper parts of the elevations and their summits, their areolae in radiating rows, rows and areolae *c.* 35 in 10 μm. Bases of linking spines linear, on the proximal half only of the summits of the elevations. No labiate process seen.

Upper Cretaceous — Campanian. Exposure XI (14), near Til'tim, basin of the river Synya, Tyumen'sk oblast, U.S.S.R. (BM 81120, SEM CB19.345–354, 3103–3125).

?Cores 22, 82, 19, near Ust'-Man'ya, basin of the river Severnaya Sos'va, Tyumen'sk oblast, U.S.S.R., (Strel'nikova, 1974).

One characteristic that distinguishes this species from all the other members of the genus except *Strelnikovia* sp. I is the outward inclination of the elevations, and this is the reason for our choice of epithet.

We have seen two specimens only of this species, one of which we have examined with the scanning electron microscope and the other, the holotype, with the light microscope. Both consist of single, somewhat eroded valves, and in that examined with the scanning electron microscope the greater part of both pseudocelli has broken away. There is a row of eroded radial ridges arranged in a semicircle around the proximal edge of the elevations in both specimens and these we interpret as the bases of linking spines. In shape of valve, this species is much closer to *Strelnikovia* sp. I than to any other member of the genus, but in that species the valve is taller and the elevations relatively shorter, and it has much sparser areolae. *S. inclinata* also resembles very closely specimens from the same material which have no trace of linking spines, one of which is illustrated as Pl. 30 fig. 5.

As pointed out (p. 328) diatoms from the basin of the river Severnaya Sos'va that Strel'nikova (1974: tabl. 39 figs 3–5) illustrated under the name *Biddulphia auliscoformis* Streln. are not conspecific with the type of that species. They have no marginal ridge and their elevations are inserted further from the apices and slope outwards. Apart from the apparent central rosette shown in fig. 3, which may be spurious, there is nothing to distinguish this specimen from *Strelnikovia inclinata*, which comes from the basin of the river Synya. Those shown in figs 4a, b, and 5 possibly belong to one of the species without linking spines that occur in these deposits but do not belong to *Strelnikovia* (see p. 289). Strel'nikova (1974) examined 42 samples of Campanian age from three cores from the basin of the river Severnaya Sos'va and reported *Biddulphia auliscoformis* from 29 of these. To what extent these records are based on *Strelnikovia auliscoformis,* or on *S. inclinata*, or on other species, including possibly both *S. reniformis* and species without linking spines, can only be decided by re-examination of her specimens. Her illustrations do, however, strongly suggest that at least some of them are based on *S. inclinata*.

5. **Strelnikovia reniformis** R. Ross & P. A. Sims, **sp. nov.** (Pl. 25 figs 1–6, Pl. 33 fig. 4)

Valva late elliptica, 65–95 μm longa, 50–75 μm lata, limbo verticali 10–12 μm alta; superficies valvae convexa, tholo centrali convexiore; valva ad centrum *c.* 42 μm alta. Elevationes maximae, mammiformes, ad apices valvae attingentes, ad vertices reniformes; altitudo ad vertices elevationum 40–50 μm, vertices 20–27 μm × 15–18 μm. Costa marginalis nulla sed area hyalina linearis inter limbum et superficiem valvae in utroque latere valvae ab altera elevatione ad alteram. Area centralis areolis irregulariter dispersis tecta, diametro *c.* 10 μm. Areolae poroides, in seriebus radialibus parum sinuatis, multum interruptis in superficie valvae, seriebus *c.* 15 in 10 μm, areolis 15–20 in 10 μm, in elevationibus infra vertices dispersae et sparsiores, in verticibus in seriebus interruptis ad axem apicalem parallelis, ut in superficie valvae distantes; in limbo in seriebus verticalibus, seriebus *c.* 16 in 10 μm, areolis *c.* 20 in 10 μm. Spinae superficiales nullae. Pseudocelli in lateribus distalibus elevationum infra vertices, transversi et medio constricti, areolis in seriebus ex linea transapicali radantibus, seriebus *c.* 25 in 10 μm, areolis *c.* 30 in 10 μm. Spinae ligantes totos vertices praeter partem minimum distalem cingentes, basibus linearibus. Rimoportula nulla visa. TYPUS: BM 81121, ex stratis cretaceis ad 'Til'tim, Tyumen'sk oblast,' Siberia.

Valve broadly elliptical, 65–95 μm long, 50–75 μm broad, with a vertical mantle 10–12 μm deep, the valve surface convex and with a central more strongly convex dome, height at the centre of the valve *c.* 42 μm. Elevations very large, mammiform, extending to the apices of the valve, with flattened kidney-shaped summits; height to the top of the elevations 40–50 μm, summit of the elevations 20–27 μm × 15–18 μm. No marginal ridge but a linear hyaline area separating the valve surface from the mantle on either side between the elevations. Central area with irregularly scattered areolae, *c.* 10 μm in diameter. Areolae poroid, in slightly sinuous, much interrupted radial rows on the surface of the valve, rows *c.* 15 in 10 μm, areolae 15–20 in 10 μm, scattered and sparser on the elevations below their summits, on the summits in interrupted rows parallel to the apical axis, their spacing as on the surface of the valve; areolae on the mantle in vertical rows, rows *c.* 16 in 10 μm, areolae *c.* 20 in 10 μm. No superficial spines. Pseudocelli on the distal side of the elevations below their summits, shaped like an hour-glass placed transversely across the distal half of the elevation, their areolae in rows radiating from a transapical line, rows *c.* 25 in 10 μm, areolae *c.* 30 in 10 μm. Bases of linking spines linear, surrounding the whole of the summits of the elevations except for a very small distal gap. No labiate process seen.

Upper Cretaceous — Campanian. Exposure XI (14), near Til'tim, basin of the river Synya, Tyumen'sk oblast, U.S.S.R. (BM 81121).

Core 82, near Ust'-Man'ya, basin of the river Severnaya Sos'va, Tyumen'sk oblast, U.S.S.R. (BM SEM CB19.363–367, CB19.369–380, CB19.701–704, 2294–2307, 3063–3080).

The shape of the summits of the elevations has suggested the specific epithet for this species.

As in the case of *Strelnikovia inclinata*, only two specimens of this species have been available to us, one of which we have examined with the scanning electron microscope and the other, the holotype, with the light microscope. In both specimens the linking spines are broken off and their bases are for the most part much eroded, but enough remains of a few to make it clear that the species possessed them (see Pl. 25 figs 5, 6). *S. reniformis* is very different from all the other species of *Strelnikovia* by virtue of the shape of its elevations, the central constriction of its pseudocellus, and the almost complete ring of linking spines on the summit of each elevation. In this last characteristic it approaches *Keratophora* Pant. and *Thaumatonema* Grev., but both these genera differ so much from *Strelnikovia*, particularly in the shape of their elevations, that the existence of this species cannot be regarded as bringing into question its generic separation from either of them.

Strelnikovia reniformis would seem to be one of the rarer species of the genus in the Campanian samples from Til'tim and Ust'-Man'ya. As we have already pointed out (p. 328 above) some of Strel'nikova's (1974) records of *Biddulphia auliscoformis* from Ust'-Man'ya may be based on this species.

6. **Strelnikovia incerta** R. Ross & P. A. Sims, **sp. nov.** (Pl. 26 figs 1–8, Pl. 33 fig. 5)

Valva lanceolata, apicibus obtusis, 50–122 μm longa, 30–45 μm lata, ad centrum *c.* 25 μm alta, sulcis duobus non profundis transversia; superficies valvae convexa, limbo continua sine ulla interruptione. Elevationes vix elevatae, centro valvae non altiores, secus axem apicalem elongatae, fines proximales rotundatas versus plerumque angustatae, 10–14 μm longae, 5–6 μm latae. Area centralis hyalina diametro 10–15 μm, nonnumquam usque ad 10 areolis penetrata. Areolae poroides, extrinsecus margine elevato, diametro *c.* 0·3 μm, in superficie valvae in seriebus radialibus multum interruptis dispositae, sed in sulcis transversis rarissimae, in limbo in seriebus non interruptis; prope marginem valvae series *c.* 18 in 10 μm, areolae *c.* 22 in 10 μm, alibi series et areolae multum sparsiores. Spinae superficiales curtae, inter se 1–3 μm, in superficie valvae sed non in limbo dispersae. Pseudocelli circulares, in parte distali elevationum, areolis in seriebus ex positione centro eorum distali radiantibus, seriebus et areolis *c.* 40 in 10 μm sed ad margines pseudocellorum sparsioribus. Spinae ligantes vertices elevationum, praeter latus distali, cingentes, basibus ellipticis, *c.* 0·6 μm longis, *c.* 0·3 μm latis. Annulus irregularis 6–10 rimoportulis formatus circum aream centralem.

TYPUS: BM 65764a, ex stratis eocaenicis superioribus ad 'Kamichev' (ut videtur 'Kamyshlov, Sverdlovsk oblast U.S.S.R.').

Valves lanceolate with obtuse apices, 50–122 μm long, 30–45 μm wide, *c.* 25 μm tall at the centre, crossed by two shallow transverse sulci; valve surface convex, continuous with and not in any way demarcated from the mantle. Elevations scarcely raised, no taller than the centre of the valve, elongated along the apical axis, usually narrowing towards their rounded proximal ends, 10–14 μm long, 5–6 μm wide. Central area hyaline, 10–15 μm in diameter, sometimes pierced by up to 10 areolae. Areolae poroid, with raised rims externally, *c.* 0·3 μm in diameter, in much interrupted radial rows on the valve surface, but very few in the transverse sulci, the rows on the mantle not interrupted, near the margin the rows *c.* 18 in 10 μm, the areolae *c.* 22 in 10 μm, elsewhere much sparser. Scattered short superficial spines 1–3 μm apart on the valve surface but not on the mantle. Pseudocelli circular, on the distal end of the elevations, their areolae in rows radiating from a point distal to their centre, rows and areolae *c.* 40 in 10 μm but sparser at the edges. Linking spines surrounding the top of the elevation except at its distal end, their bases elliptical, *c.* 0·6 μm long, 0·3 μm broad. An irregular ring of 6–10 labiate processes at the outer edge of the central hyaline space.

Upper Eocene. 'Kamichev' (presumed to be Kamyshlov, Sverdlovsk oblast, U.S.S.R.) (BM 65764a holotype, SEM CB15.358–367, CB16.515, CB16.522–523, CB16.534–536, CB16.781–784, CB16.787–788, CB16.791–792, 1905–1927, 1940–1942, 2985–2986).

All the specimens of this species that we have seen consist of single valves with a row of what appear to be the broken bases or lower parts of interlocking linking spines around all but the distal end of their elevations, but not enough remains of any of these to show with certainty that this interpretation is correct. Nevertheless, the specimens have all the other characteristics of *Strelnikovia* and there is certainly no other genus of diatoms to which they might belong. We have therefore included them here but have chosen a specific epithet that reflects this slight uncertainty.

Strelnikovia incerta differs from all the other species of the genus in possessing two transverse sulci and also in having a ring of labiate processes in the centre of the valve. The only other species of *Strelnikovia* in which labiate processes have been seen is *S. antiqua*, where they are fewer in number and close to the margin of the valve. However, we have not seen the interior of *S. tumida, S. inclinata, S. reniformis*, or the species for which we have insufficient material to propose a name. We therefore do not consider that, in the present state of our knowledge, we would be justified in erecting a new genus for this species on the basis of these two differences alone.

The existence of this species in the upper Eocene extends the duration of the genus very considerably. It is perhaps surprising that no member of the genus has been encountered in deposits intermediate in age between the upper Cretaceous and the upper Eocene, but little is known about the diatom flora in the area from which all specimens of *Strelnikovia* have come, the eastern slopes of the Ural mountains.

Strelnikovia sp. I (Pl. 27 figs 1–8)

Biddulphia robusta sensu Strel'nikova, *Diat. pozdn. Mela* (*Zap. Sibir'*): 93, t. 39 figs 1–2 (1974), non Pant.

Frustules with the pervalvar axis longer than the apical axis. Valve elliptical, 70–140 μm long, 40–85 μm broad, with a vertical mantle *c.* 15 μm deep, but deeper at the apices, not sharply delimited from the valve surface; valve surface rising to a rounded ridge joining the two elevations, height at the centre of the valve *c.* 40 μm. Elevations stout, arising somewhat proximal to the apices and inclined towards these, circular in cross section and somewhat expanded above; height to the top of the elevations *c.* 50 μm, diameter of the elevations *c.* 15 μm. No marginal ridge. Areolae poroid, sparsely scattered over the valve surface and mantle, sometimes forming one, or two contiguous, rings in the centre of the valve and sometimes denser on the proximal side of the elevations. Pseudocelli on the distal side of the expanded tips of the elevations, the areolae in rows radiating from a transapical line in the centre of the pseudocellus, rows and areolae *c.* 33 in 10 μm, sparser at the margins of the pseudocelli. Linking spines around all but the distal side of the summit of the elevations, their bases linear and *c.* 0·3 μm wide, their upper part *c.* 0·8 μm wide. No labiate process seen. Mature cingulum of at least three open bands with ligulae at alternate apices, densely areolate with areolae in vertical rows, areolae and rows *c.* 22 in 10 μm.

Upper Cretaceous — Campanian. Core 82, near Ust'-Man'ya, basin of the river Severnaya Sos'va, Tyumen'sk oblast, U.S.S.R. (BM SEM CB8.449–453, CB8.455–468, CB8.767–775, CB16.588–598, 2193–2212, 5471–5494; Strel'nikova 1974). Core 19, same locality (Strel'nikova, 1974).

Unfortunately we have found only one specimen of this species, and this we examined with the scanning electron microscope. As there is in consequence no permanently mounted specimen that we can designate as holotype, we have not given this species a name.

The one specimen that we have examined consists of a single valve with a number of girdle elements attached. These are not the cingulum of that valve, which is apparently a hypovalve, but are part of the cingulum of the corresponding epivalve; one of them surrounds the mantle of the valve and there are the eroded remains of another band along its free edge (Pl. 27 figs 1–3). Most of the linking spines are broken off, leaving only their radiating linear bases, but a few survive intact (Pl. 27 fig. 4).

In shape of valve this species resembles *Strelnikovia inclinata*, but its very sparse areolation distinguishes it readily. The specimens illustrated by Strel'nikova (1974: tabl. 39 figs 1–2) under the name *Biddulphia robusta* Pant. differ in two respects: they apparently have some scattered spines on the valve and the pseudocelli cover the whole summits of the elevations, not just their distal parts. The resemblances are, however, so strong that we regard these differences as no more than infraspecific variation. There can be no doubt that the diatom illustrated by Strel'nikova is a *Strelnikovia*; the bases of the linking spines can be clearly seen in her fig. 1b.

Biddulphia robusta Pantocsek (1889: 86, taf. 12 figs 203, 205) with which Strel'nikova (1974) identifies this species is a true *Biddulphia* sensu stricto, with a deep depression between its elevations, not a raised ridge, and it has on either side a hyaline marginal ridge connecting the two elevations that is much taller than the central part of the valve. *Biddulphia nobilis* Brun (in Brun & Tempère, 1889: 27, pl. 5 fig. 11), which Strel'nikova (1974) mentions as closely allied, is synonymous with the true *Biddulphia robusta* Pant. (Brun in Tempère, 1893) and is also not related to *Strelnikovia* Sp. I.

Strel'nikova (1974) records this species from only five of her 42 samples from the Campanian of Ust'-Man'ya in the basin of the river Severnaya Sos'va, and our only specimen also comes from there. It is thus a comparatively rare species in the material of that age from that locality.

IV. ***KERATOPHORA*** Pant., *Beitr. Kenntn. Foss. Bacill. Ungarns* **2**: 85 (1889); De Toni, *Syll. Alg.* **2**: 898 (1894) [*'Ceratophora'*].

Frustules united in straight inseparable chains. Valves bipolar, with cylindrical, more or less sinuous elevations arising from two transverse hyaline ridges or from two hyaline areas. Areolae poroid. Pseudocelli large, on the distal side and summit of the elevations. A complete ring of interlocking linking spines on the summit of the elevations, their bases linear and radiating from the centre of the elevations, their upper parts wider, triangular in side view. No labiate processes seen. Mature cingulum of at least two elements, one of them, perhaps both, an open band.

TYPE SPECIES: *Keratophora nitida* Pant., loc. cit. (lectotype designated here by us.).

Pantocsek, when establishing the genus, included in it two new species, *Keratophora nitida* and *K. robusta*, both from Kuznetsk, Penza oblast, U.S.S.R., a deposit almost certainly of upper Eocene age. Whilst the first of these is obviously a diatom, the second is not, unless the illustration of it (Pantocsek, 1889: taf. 16 fig. 277) is much more inaccurate than other figures in the same work. Pantocsek included the genus in the Bacillariaceae, i.e. in a taxon equivalent to the class Bacillariophyceae as currently recognized, and this must be regarded as part of its protologue. Accordingly, *K. nitida* is the only possible lectotype for the genus, and it is here designated as such by us.

Tempère (1893) says of Pantocsek's figure of *Keratophora nitida* 'est une plaque silicieuse et non une Diatomée' and Brun in his list of corrections to Pantocsek's work included in Tempère's paper also says that the figure does not represent a diatom, attributing this opinion to De Toni, but neither Tempère nor Brun make any mention of the figure of *K. robusta*. De Toni (1894), however, in a part of the *Sylloge Algarum* published in the following year, repeats Pantocsek's diagnoses of the genus and the two species in slightly modified form but does not express any doubt about either species being a diatom. His views on correct latinity caused him to alter the spelling of the generic name to *Ceratophora*, and this incorrect spelling has been used subsequently by most authors. As Pantocsek's figure of *K. nitida* is quite obviously of the diatom described under that name in this paper, it is very remarkable that both Tempère and Brun should have considered that it was not a diatom and that they should at the same time have made no comment on *K. robusta*. It is tempting to suppose that their remarks were really intended to apply to *K. robusta* but were made of *K. nitida* as a result of some confusion.

It might be thought that the statements by Tempère and Brun that *Keratophora nitida* was not a diatom were equivalent to the choice of *K. robusta* as the lectotype of the genus. However, even if that view be held, the choice is to be superseded because it was 'based on a misinterpretation of the protologue' (*International Code of Botanical Nomenclature*, Art. 8.1).

As far as our present knowledge goes, the genus is monotypic. *Keratophora granulata* (Chenev.) Meister (1937) is a synonym of *K. nitida* as is *K. russica* Pant. ex Jousé (in Proshkina-Lavrenko et al., 1949*b*). *K. nuda* Meister (1937) is the spore of a *Hemiaulus*, as Pl. 29 fig. 8 shows. Jousé (in Proshkina-Lavrenko et al., 1949*b*: 205) treats *Hemiaulus perlongus* Pantocsek (1889: 82, taf. 20 fig. 315) as a synonym of *K. robusta* but her illustrations (tabl. 77 fig. 3a, b) are of a species of *Dicladiopsis*. Their probable identity is discussed under that genus (p. 323 above).

Cleve-Euler (1951: 127) describes and figures two diatoms as '*Ceratophora* sp. 1' (op. cit.: fig.

290) and '*Ceratophora* sp. 2' (op. cit.: fig. 291a). Neither of these is a *Keratophora* and the illustration of the second suggests that it is a phytolith; we can make no suggestion about the genus to which the first belongs.

1. **Keratophora nitida** Pant., *Beitr. Kenntn. Foss. Bacill. Ungarns* **2**: 85, t. 17 fig. 280 (1889); P. A. Sims in *Bacillaria* **3**: 40 (1980). (Pl. 28 figs 1–7, Pl. 29 figs 1–7)

Biddulphia rossica Pant., tom. cit.: 85, t. 20 fig. 316 (1889).

Kittonia granulata Chenev. in *Bull. Soc. fr. Microsc.* **3**: 104, t. 5 figs 4–5 (1934); Jousé in Proshkina-Lavrenko et al., *Diat. Anal.* **2**: 182, t. 95 fig. 7a, b (1949), in *Bot. Mater. Inst. sporov. Rast. bot. Inst. Komarova* **10**: 95, t. 6 fig. 1 (1955).

Keratophora granulata (Chenev.) Meister in *Ber. schweiz. bot. Ges.* **47**: 259, t. 4 figs 4–5 (1937) '*Ceratophora*'; Hustedt in A. Schmidt, *Atlas Diat.*: t. 434 figs 5–10 (1940); Brigger & Hanna in *Occ. Pap. Calif. Acad. Sci.* **50**: 8 (1956).

Keratophora russica Pant. ex Jousé in Proshkina-Lavrenko et al., *Diat. Anal.* **2**: 206 (1949), nom. superfl.

Frustules rectangular in girdle view, the pervalvar axis probably equalling or exceeding the apical axis, united in inseparable chains by interlocking linking spines on the summits of the elevations. Valves lanceolate to broadly lanceolate with obtuse apices, 47–140[–170] μm long, 32–90[–140] μm broad, the valve surface sometimes gently convex throughout, sometimes slightly depressed adjacent to the margin but elsewhere gently convex, normally crossed by two hyaline rounded ridges slightly curved towards the centre of the valve, the ridges almost contiguous at the valve centre to separated by about 1/2 of the length of the valve; mantle vertical, 8–11 μm deep, hyaline except for a few areolae at the apex, sometimes surmounted by a thin marginal ridge up to 6·5 μm tall. Elevations arising from the hyaline transapical ridges or from hyaline areas, tubular, inclined towards the apices, sinuous, usually very markedly so but infrequently inclined outwards but only very slightly sinuous, at their tips vertical, somewhat swollen and elliptical in cross section, height to the top of the elevations 25–100 μm, diameter of the stem of the elevations 4–10 μm, their tips 12–20 μm × 7–13 μm. Areolae poroid, with a raised external rim, scattered throughout or in radial rows near the margin and scattered elsewhere, rows and areolae 8–12 in 10 μm, areolae sparser where scattered; elevations hyaline. Scattered small superficial spines 3–4 in 10 μm. Pseudocelli on the summit and all but the proximal side of the swollen tips of the elevations, their areolae in rows radiating from their centre, rows and areolae 24–28 in 10 μm. Each cingulum consisting of at least two elements, the pleura *c.* 20 μm deep and with a ligula, the one copula seen an open band *c.* 14 μm deep; both bands with hyaline advalvar and abvalvar margins 2–4 μm deep, elsewhere with very small areolae in vertical rows, rows and areolae 12–14 in 10 μm.

[Lower — upper Eocene. 'Carlovo', U.S.S.R. (BM 36231) (doubtful record, see p. 281 above).]

Middle Eocene. Bermuda Rise, 30° 53.39′ N, 67° 38.86′ W. Deep Sea Drilling Project, Leg. 1, Site 6, core 4 (BM 78499).

Upper Eocene. Kuznetsk, Penza oblast, U.S.S.R. (BM 32737, coll. Adams TS693; PH Gen. coll. 35196; Pantocsek 1889).

'Kamichev' (presumed to be Kamyshlov, Sverdlovsk oblast, U.S.S.R.). (BM 35045, 36229, 63882, 63883, 63884, 65766b, 65767b, 65768, 65769, 78388, 81122, 81123, coll. Adams, H890, H945, TS746, TS747, TS749, SEM B17.903–905, B17.953, B17.956, B27.883–892, CB13.707–709, CB13.711–712, CB13.714–716, CB15.310–321, CB15.323–324, CB15.326–332, CB15.334–351, CB16.777–778, CB16.780, CB16.785, 1928–1939, 2422–2451, 2962–2978, 4085–4097, 9617–9621; Chenevière, 1934; Meister, 1937; Hustedt, 1940; Jousé, 1955*; Brigger & Hanna, 1965).

Pavlodar, U.S.S.R. (for this locality see p. 281 above) (Jousé, 1955).

It is by no means easy to make out the structure of the girdle in this species from the damaged remains that are present on a few of the specimens studied with the scanning electron microscope. One specimen has a well developed ligula on a band that is probably a pleura (Pl. 28 fig. 6). There is another band advalvar to this with a very unusual structure; what is obviously the open end of the pars exterior of the band seems to be fused for part of its length with a closed band below that extends not only some 6 μm in a (presumed) advalvar direction but also the same distance in an abvalvar direction, so that well over half the depth of the areolate pars exterior is underlain by a hyaline sheet of silica. We can find no previous account of girdle bands with such a structure and it would seem that the underlying part is actually the mantle and marginal ridge of a hypovalve with which the band has become fused by a diagenic process during fossilization. Because of this possibility we have not made any mention of this band in our formal description of the species.

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*This record is from Kamyshlov, not 'Kamichev'.

Pantocsek's (1889: taf. 17 fig. 280) illustration of *Keratophora nitida* is of a specimen in which the tops of both elevations have broken off, and the long spine shown on the end of one of them is a detached fragment and not part of the valve. This is a specimen in which the elevations arise nearer the centre of the valve than in most. On the other hand, the specimen illustrated as *Biddulphia rossica* (Pantocsek, 1889: taf. 20 fig. 316) has one elevation intact and the ring of bases of interlocking linking spines is clearly shown. In this specimen the elevations arise as near the apices of the valve as in any. There is thus considerable difference between these two specimens, but when many are available it becomes clear that they represent the extremes of a continuous range.

Pantocsek (1889: 85) expressed doubt about the generic placing of *Biddulphia rossica*, saying of it 'Probabiliter *Keratophora*'. Jousé (in Proshkina-Lavrenko et al., 1949*b*) was apparently the first to realize that *Biddulphia rossica* was a synonym of *Keratophora nitida*, for she calls the species '*Keratophora russica* Pant.' citing *K. nitida* Pant. as a synonym. However, the combination *Keratophora rossica* had not been published previously and Jousé did not give any sufficient indication that it was based on *Biddulphia rossica* Pant. Her remark that the species might belong to the genus *Biddulphia* is not enough for this, even when Pantocsek's suggestion that his *Biddulphia rossica* might be a *Keratophora* is taken into account. *Keratophora russica* Pant. ex Jousé must therefore be regarded as a newly published name and an illegitimate superfluous substitute for *K. nitida*, rather than as a validly published and legitimate new combination which must be adopted because Jousé was the first to choose one of two simultaneously published synonyms.

When Chenevière (1934) found specimens of this species in the material from 'Kamichev', in which it is comparatively common, he described it as a new species of *Kittonia*. Hustedt recognized that it was congeneric with *Keratophora nitida*, although he did not realize its specific identity. He communicated this to Meister, who published the new combination *Keratophora granulata*, antedating Hustedt's own publication of the same combination.

A small proportion of the specimens of this species have elevations that are much taller than those found on the great majority and are also not very sinous (Pl. 29 figs 4–6), although they arise comparatively close to the centre of the valve. The height to the top of the elevations in these specimens is 55–100 μm, whilst in the others it does not exceed about 40 μm. We have found none of these specimens with very tall elevations joined together as sibling pairs, and one of the two that we have been able to examine with the scanning electron microscope has rather poorly developed linking spines; on the other only the eroded bases of the linking spines remain. It seems possible that these specimens with exceptionally tall elevations may be separation valves.

There are also occasional specimens in which the transverse rounded ridges are virtually absent (Pl. 29 figs 1, 2). In these specimens the elevations arise nearer the apex than in most and are only very slightly sinuous, but they are not particularly tall. There are other specimens (Pl. 29 fig 3) transitional between these and the more frequent ones where the elevations arise much closer to the centre of the valve and are very sinuous. We see no case, therefore, for distinguishing the two forms at any taxonomic level. Most of the specimens without transverse ridges are in the middle part of the size range of the species. However the specimen at PH, Gen. coll. 35196, the largest we have seen, is also of this type. Its valve is broadly elliptical, 170 μm long, 140 μm broad, and gently domed. There are no transverse raised ridges, but a hyaline area *c.* 30 μm in diameter around the base of each elevation. These bases are *c.* 90 μm apart, i.e. they are separated by more than half the length of the valve. The elevations are comparatively short, inclined towards the apices of the valve, scarcely, if at all, sinuous, and strongly contracted just below the tips. The areolae are very irregularly scattered and are sparse, only 1–5 in 10 μm. The large size and anomalous structure of this specimen suggests to us that it is probably an initial valve. Because its dimensions are outside the normal range of the species, we have given them in square brackets in the description.

Another feature that is very variable is the marginal ridge. This may be very strongly developed, surrounding the whole valve and rising to a height of up to 6·5 μm, or there may be virtually no sign of any such ridge being present. Some pairs of sibling valves have one valve with a strongly developed marginal ridge and one in which it is virtually absent (Pl. 29 fig. 7). When a well developed marginal ridge is present, the valve surface is somewhat depressed within it; when there is no marginal ridge, the valve surface is convex throughout.

Whilst there is some uncertainty about the geological age of specimens of *Keratophora nitida* from Kuznetsk, Pavlodar, 'Carlovo', and 'Kamichev', there is no strong indication that any of these records represents an extension outside its firmly dated range from middle to upper Eocene, especially as there is doubt about the correctness of the record from 'Carlovo'. The middle Eocene record is based on its presence in the material of that date recovered from the Bermuda Rise by the Deep Sea Drilling Project. The flora accompanying it there shows strong similarities to that of contemporary deposits on Barbados, but *K. nitida* has never been reported from there. All the other records of the species come from the U.S.S.R., from the Volga basin, from the east of the Urals and probably from the Ukraine.

Species excludenda:

Keratophora robusta Pant., *Beitr. Kenntn. foss. Bacill. Ung.* **2**: 85, t. 16 fig. 277 (1889), quae species Bacillariophycearum non est.

Keratophora nuda Meister in *Ber. schweiz. bot. Ges.* **47**: 259, t. 4 fig. 3 (1937), *'Ceratophora'*, quae *Hemiaulus* sp. est.

Meister's name is based on a spore of a species of *Hemiaulus* Heib., as Pl. 29 fig. 8 shows. This *Hemiaulus* is characterized by the diminution in size of the areolae towards the margin of the valve. We have found only four illustrations of fossil *Hemiaulus* spp. that show a similar diminution. One is by A. Schmidt (1889: taf. 143 fig. 38) of a specimen identified as *H. weissei* Grunow from Simbirsk (now Ulyanovsk), U.S.S.R., but the original illustration of this species (Grunow, 1884: taf. 5 fig. 52), which is of a specimen from Mors, Denmark, does not show this character. The other three are by Jousé (1977: tabl. 82 figs 1–3) of specimens from the upper Cretaceous of the subantarctic zone of the Pacific Ocean identified as *Hemiaulus kittonii* Grunow. However, Grunow's original illustrations of this species (in Van Heurck, 1883: pl. 106 figs 6–9) are of specimens from Mors, Denmark, which do not show this characteristic and which also show that this species has a very different spore. *Hemiaulus* sensu stricto, and in particular its fossil species, is in need of a thorough revision, and the specific identity of *Keratophora nuda* must remain uncertain until this is done.

V. ***THAUMATONEMA*** Grev. in *Trans. microsc. Soc. Lond.* II, **11**: 76 (1863).

Frustules united in straight inseparable chains. Valves circular to broadly elliptical with two elevations arising either separately from a central hyaline space or two almost contiguous hyaline spaces, or diverging from the summit of a single central vertical tube, tubular, sloping outwards and reaching almost or quite as far as the margin of the valve, with vertical and somewhat expanded tips. Areolae loculate, in radial rows. Pseudocelli covering the whole of the distal part of the expanded tips of the elevations. A complete ring of interlocking linking spines on the summit of the elevations, their bases linear and radiating from the centre of the elevations, their upper parts wider, triangular in side view. Labiate processes not seen. Mature cingulum, known only in one species, of at least three elements.

TYPE SPECIES: *T. barbadense* Grev., loc. cit.

This genus was established by Greville for one species, *Thaumatonema barbadense*, which is thus its type. He added a second species, *T. costatum*, two years later and no others have yet been found; *T. complanatum* Brun is a synonym of *T. barbadense*.

There is considerable resemblance between the elevations of this genus and those of *Keratophora*; in both genera these have sinuous cylindrical hyaline stems, a complete ring of very similar linking spines around their summits and well developed pseudocelli on the distal halves of their tips. However, not only the shape of the valve but also the arrangement and nature of the areolae differ so markedly between the two that there is good reason for maintaining them as separate genera. In *Keratophora* the areolae are poroid, well separated from one another, and scattered irregularly over most or all of the valve, whilst in both species of *Thaumatonema* they are loculate, closely packed over most of the valve and arranged in radial rows, except sometimes very close to the centre.

The genus is known only from the oceanic beds of Barbados and from the middle Eocene material recovered from the Bermuda Rise by the Deep Sea Drilling Project. The dating of the specimens from the oceanic beds of Barbados is in some cases uncertain, but the genus had a range at least from the middle Eocene up to the Eocene–Oligocene boundary. Whether it persisted later into the Oligocene is, however, still an open question.

Key to the species

1a Valves without narrow hyaline spaces radiating from the central area .... 1. ***barbadense*** (p. 337)
1b Valves with narrow hyaline spaces radiating from the central area .... 2. ***costatum*** (p. 338)

1. **Thaumatonema barbadense** Grev. in *Trans. microsc. Soc. Lond.* II, **11**: 76, t. 5 fig. 26 (1863). (Pl. 33 figs 6, 7)

Thaumatonema complanatum Brun in *Diatomiste* **2**: 244, t. 19 fig. 5 (1896).

Frustules rectangular in girdle view, the pervalvar and apical axes of about equal length. Valves circular to broadly elliptical, 20–70 μm long, 16–60 μm broad, with a vertical mantle 3–8 μm deep, surface rising slightly from the margin but, except in the smallest specimens, slightly depressed proximal to this, and with a central hyaline boss. Elevations either arising separately from the central boss or united at their bases as a vertical hyaline tube up to 15 μm tall, reaching almost or quite to the margin of the valve, sloping upwards at less than 45° to the valvar plane, tubular and 2·5–4 μm in diameter, turned upwards and expanded at their tips, the expanded tips elliptical, *c.* 14 μm × 5 μm, their long axis parallel to the valve margin. A circular to elliptical hyaline central area, diameter *c.* 1/3rd that of the valve, absent in the smallest specimens. Areolae loculate, close packed and sub-hexagonal, in radial rows, rows and areolae 9–11 in 10 μm, rows continuing onto the mantle, but a hyaline band *c.* 2 μm wide around the valve at its free edge. A ring of spines 3–4 μm tall and 4–5 in 10 μm around the margin of the valve. Pseudocelli covering all but the proximal side of the expanded tips of the elevations, their areolae *c.* 20 in 10 μm. Linking spines in a complete ring around the summits of the elevations, linear and very narrow at the base but expanded above. Mature cingulum of at least three elements, with vertical rows of areolae, rows and areolae *c.* 16 in 10 μm.

Middle Eocene. Cambridge, Barbados (BM 2791, 2853 holotype, 3090, 3419, 3423, 3431, 3472, 10456, 13766, 50081, coll. Adams F1244; Greville 1863).
Bermuda Rise, 30° 35.39′ N, 67° 38.86′ W. Deep Sea Drilling Project, Leg. 1, Site 6, core 4 (CAS 43151).
Eocene–Oligocene boundary. Joe's River, Barbados (CAS).
Middle Eocene–early Miocene. Mount Hillaby, Barbados (Brun, 1896).

All the specimens of this species that we have had available have been mounted and we have therefore been able to examine it with the light microscope only. We are in consequence, not completely certain that its areolae are loculate, although they appear to be so.

There is considerable variation in the insertion of the elevations, with a continuous series from specimens in which they arise separately with their bases up to 15 μm apart, through those with contiguous bases, to those in which they arise as a single hyaline tube which bifurcates at up to 15 μm from the valve surface. The holotype of *Thaumatonema barbadense* is at the latter extreme of the range, whereas *T. complanatum* is based on a specimen from near the other extreme. The specimens that we have seen, however, some 15 in all, show that the differences between these two are no more than individual variations within a continuous series and there is only one species involved.

Thaumatonema barbadense ranges in age at least from the middle Eocene up to the Eocene–Oligocene boundary. Whether the sample from Mount Hillaby, Barbados, in which Brun (1896) found the holotype of *T. complanatum*, came from a stratum outside this age range is not known, but there is a possibility that it is later in date than that from Joe's River, Barbados.

2. **Thaumatonema costatum** Grev. in *Trans. microsc. Soc. Lond.* II, **13**: 97, t. 8 fig. 3 (1865). (Pl. 33 figs 8, 9)

Valve circular to broadly elliptical, 45–95 μm long, 40–85 μm broad, surface slightly convex distal to a central boss. Elevations arising separately from the central boss, reaching almost or quite to the margin of the valve, sloping upwards at less than 45° to the valvar plane, hyaline, tubular, 3–4 μm in diameter, turned upwards and expanded at their tips, the expanded tips elliptical, 10–12 μm × 5–9 μm, their long axes parallel to the valve margin. A single small elliptical hyaline area between the bases of the elevations, or, when these are further apart, two almost contiguous hyaline areas each surrounding the base of an elevation. Areolae loculate, in radial rows, distal to the central boss separated into 9–20 sectors by linear hyaline areas which narrow towards the margin and become internal costae, rows and areolae 10–15 in 10 μm near the margin of the valve, more widely spaced towards its centre. Pseudocelli covering all except the proximal side of the expanded tips of the elevations, their areolae *c.* 20 in 10 μm. Linking spines in a band around the whole summit of the elevations, narrow and linear at the base.

Middle Eocene. Cambridge, Barbados (BM 3419 holotype; Greville 1865c)

Bermuda Rise, 30° 35.39′ N, 67° 38.86′ W. Deep Sea Drilling Project, Leg. 1, Site 6, core 4 (BM 78500; CAS 43151).

For this species also all the specimens available to us have been mounted, and we have been able to examine them with the light microscope only. We are therefore not quite certain in this case also that the areolae are loculate, although they have every appearance of being so.

This species is apparently even rarer in the oceanic beds of Barbados than *Thaumatonema barbadense*; it seems that the holotype is the only specimen from there that has been found. It is also the rarer of the two species of the genus in the material recovered from the Bermuda Rise. Both localities from which specimens of *T. costatum* have come are dated as middle Eocene. With species as rare as it is, however, there must be uncertainty about the relation between its known distribution in time and space and its actual one.

Discussion

We have grouped together the five genera that we describe in this paper because they resemble one another more closely than they do any other members of the Hemiauloideae. We have discussed (p. 286) the characters that separate them from the other members of the subfamily with interlocking linking spines and from *Hemiaulus* Heib. itself. They bear even less resemblance to other genera of the subfamily, e.g. *Eucampia* Ehrenb. and *Cerataulina* Perag. ex Schütt. However, as we point out below, there is a possibility that the five genera dealt with here may not form a monophyletic group.

There are comparatively few differences between the valves of *Dicladiopsis* with linking spines and the species of *Briggera* with elliptical valves, but, as we argue (p. 318), these differences combined with the indications that the species of *Dicladiopsis* normally have heterovalvar frustules are an adequate basis for generic separation. In spite of the possibility that all the species of *Dicladiopsis* may be resting spores, there can be little doubt about there being a close phylogenetic relationship between that genus and *Briggera*. There are, however, considerable differences in the shape, number and position of the linking spines between *Briggera* and *Dicladiopsis* on the one hand and *Strelnikovia, Keratophora,* and *Thaumatonema* on the other. These three genera differ considerably from one another, but they all differ from *Briggera* and *Dicladiopsis* in various ways in their elevations, the shape and contour of their valves, and their areolation, as well as in their linking spines.

The elevations, pseudocelli, and linking spines of *Keratophora* and *Thaumatonema* are virtually identical, apart from the fusion of the bases of the elevations in some specimens of *T. barbadense*, but the shape and contour of their valves and their areolation differs very considerably. However, it seems most unlikely that a structure so unusual as the tubular hyaline elevations with pseudocelli and interlocking linking spines would have come to be virtually identical by convergence. On the other hand it seems clear that poroid areolae have evolved into loculate ones many times in the evolutionary history of the diatoms; this is almost certainly a change dictated by considerations of mechanical strength when areolae become more closely packed.

Strelnikovia differs considerably from *Keratophora* and *Thaumatonema* in the shape of its elevations and the fact they are not hyaline, and also in the shape and contour of its valves. However, its linking spines are identical in shape with those of *Keratophora* and *Thaumatonema* and they are also as numerous as in these two genera. There seems no obstacle to supposing that all three genera have a close common ancestor, and even the possibility that *Keratophora* and *Thaumatonema* evolved from *Strelnikovia* between the upper Cretaceous and the middle Eocene cannot be ruled out.

Problems are raised, however, by the existence of distinct species with all the characters of either *Briggera* or *Strelnikovia* except for linking spines. The difficulty of distinguishing between such species and separation valves of those two genera has been discussed (pp. 288–290). Any classification based on number of characters in common would group at least species 1–8 of *Briggera* (*B. includens, B. morenoensis, B. siberica, B. monoligata, B. capitata, B. vemae, B. affixa*, and *B. robusta*) with *Biddulphia novae-zealandiae* Wise and the two species illustrated as Pl. 30, figs 3, 4, and the species of *Strelnikovia*, except perhaps *S. incerta*, with the species illustrated as Pl. 30 figs 5–8. Not only *Briggera includens* and all the species of *Strelnikovia* except *S. incerta,* but also the un-named species without linking spines just referred to, occur in the Campanian deposits of the eastern Urals. This is the earliest fossil diatom flora to be well known, and we thus have no information about the earlier evolutionary history of these species, although we know that *B. includens* dates back at least to the early Coniacian. There are two possible courses that this evolution may have taken.

There may have been a parent stock with interlocking linking spines that was ancestral to both *Briggera* and *Strelnikovia*, and, after these two genera had diverged, they may each independently have given rise to species without linking spines. Modern genera that occur in inseparable chains (e.g. *Chaetoceros* Ehrenb., *Bacteriastrum* Shadb., *Cymatosira* Grunow, *Campylosira* Grunow ex Van Heurck) are normally planktonic, as are most of those in which the sibling valves are in close contact although not inseparably united (e.g. *Rhizosolenia* Brightw. and *Hemiaulus* Heib.), whilst epiphytic genera that occur in chains normally have their frustules united by mucous pads at one corner (e.g. *Biddulphia* Gray, *Striatella* Agardh). There are thus grounds for suggesting that *Briggera* and *Strelnikovia* may have been planktonic genera that both independently gave rise to epiphytic forms without linking spines. We (Ross & Sims, 1973: 113) have previously suggested that the Hemiaulaceae and the Biddulphiaceae, which we then regarded as separate families, diverged from a common stock as a result of adaptation to a planktonic and a littoral habitat respectively.

On the other hand, *Briggera* and *Strelnikovia* may have evolved independently from different ancestors, the fact that they both possess interlocking linking spines being an example of convergence. Very similar linking spines occur in diatoms that are not closely related to *Briggera* and *Strelnikovia*, e.g. *Trinacria exsculpta* (Heib.) Hust. (Ross, Sims & Hasle, 1977) and *Melosira granulata* (Ehrenb.) Ralfs (Crawford, 1979), and it is thus reasonably certain that this structure has evolved more than once.

There is little evidence on which to base a choice between these two possibilities. Simonsen

(1972) suggested that two characters found in some members of the Hemiaulaceae, viz.: resting spores and heterovalvar frustules, indicated that it was a more primitive family than the Biddulphiaceae. We, however, continue to adhere to our view expressed earlier (Ross & Sims, 1973) that it is an open question whether or not the common ancestor of these two groups had linking spines. Very much more than our present knowledge of the fossil history of the diatoms before the upper Cretaceous is needed before any firmly based opinion on this can be expressed.

The fact that *Briggera* and *Strelnikovia* resemble much more closely the species illustrated as Pl. 30 figs 3, 4 and Pl. 30 figs 5–8 respectively than they do each other or any other members of the Hemiauloideae, and that these un-named species resemble either *Briggera* or *Strelnikovia* more closely than they resemble other members of the Biddulphioideae, indicates that one or other subfamily is polyphyletic. It would thus seem that a division of the Biddulphiaceae into two subfamilies on the basis of the presence or absence of linking spines should be abandoned. In this we agree with Glezer (1979), although we have considerable reservations about the sub-orders and tribes within the Biddulphiaceae that she proposes. Many more species than hitherto will have to be examined in detail before there is a satisfactory basis for grouping the genera within this family. This will almost certainly result in revision of the limits of at least the larger genera as well as bringing a new grouping of these within the family. It is, for instance, unlikely that the very large group of species hitherto included in *Triceratium* Ehrenb., for which Glezer (1975) has proposed the genus *Sheshukovia*, will prove to belong to a single genus, and even more unlikely that *Briggera* will be included in a taxon that includes *Cerataulina* H. Perag. ex Schütt (see Hasle & Syvertsen, 1980 for the structure of this genus) and *Eucampia* Ehrenb. (see Syvertsen & Hasle, 1983), but excludes *Biddulphia* Gray.

Most of the 31 taxa described in this paper come from relatively high latitudes. 22 of them have been found only at localities nearer the poles than 45° N or 45° S, six of them only between these latitudes and three at latitudes both higher and lower than 45°. Furthermore, 19 of these 31 taxa have been found in the U.S.S.R., in the Ukraine and the Volga basin, and on the eastern slopes of the Urals and the adjacent parts of the west Siberian lowland, that is to say in deposits laid down in the epicontinental sea that in upper Cretaceous and Paleogene times occupied the area between Asia and Europe. *Strelnikovia* is confined to this area, as are four of the five species of *Dicladiopsis*, the remaining one coming from the Caribbean. The single species of *Keratophora* occurs in the U.S.S.R. and the western Atlantic at about 30° N, where *Thaumatonema*, otherwise known only from the Caribbean, also occurs. *Briggera*, the largest of the genera with which we are concerned, has a world-wide distribution, with the majority of its species occurring in higher latitudes. The deposits in which these genera have been found all appear to have been laid down in comparatively shallow water. The evidence thus suggests that they were all members of the neritic plankton and that all, except *Thaumatonema*, occurred primarily in cooler water. However, it is impossible to say to what extent their known distributions represent the actual distributions of the taxa concerned or are a consequence of the distribution of samples of a relevant age that have been found and studied in sufficient detail. Ten of the taxa described here are known only from material that has relatively recently become available for study, either the upper Cretaceous material from the eastern Ural mountains first studied by Jousé (1948) and more thoroughly investigated by Strel'nikova (1974), or the cores taken by the R/V Vema in the south-western Atlantic. The number of novelties found in both these (see Strel'nikova, 1974 for the former; and Hanna, Hendey & Brigger, 1976; Hendey & Sims, 1984; Ross, 1976; Ross, Sims & Hasle, 1977 for the latter) indicates how much more information further samples might yield. By now many samples of upper Cretaceous and Paleogene age containing diatoms have been recovered by coring or dredging from the bed of the oceans but these have so far been studied primarily by stratigraphers and paleo-ecologists, who are interested almost exclusively in the species that occur more frequently. The search of these samples for the rarer species within them, whilst it might yield little of stratigraphical importance, could greatly enhance our knowledge of the taxonomy, paleogeography, and evolutionary history of the diatoms.

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Description of plates

Plates 1–30 are SEM micrographs.
Plates 31–33 are LM micrographs.

Plate 1. *Briggera includens* (Grunow) R. Ross & P. A. Sims. Figs 1, 3, 5, 7, 8: 'Carlovo', U.S.S.R. Figs 2, 4, 6, 9: Core 82, near Ust'-Man'ya, Tyumen'sk oblast, U.S.S.R. Fig. 1: two sibling valves, girdle view, × 1050. Fig. 2: ditto, × 950. Fig. 3: ditto, × 775. Fig. 4: same specimen as fig. 2, oblique view, × 1125. Fig. 5: two sibling valves, oblique girdle view, specimen *c.* 100 μm long with shallow sulci across the projections just proximal to the elevations, × 725. Fig. 6: same specimen as fig. 2, oblique view showing labiate processes, × 875. Fig. 7: elevations of two sibling valves showing shape of linking spines and Crawford step on lower valve, × 2000. Fig. 8: central portion of valve showing single peg projecting into some areolae, × 5000. Fig. 9: as fig. 7, × 1700.

Plate 2. *Briggera morenoensis* R. Ross & P. A. Sims. Moreno Gulch, Fresno County, California, U.S.A. Fig. 1: oblique view of complete frustule just following division and one attached valve, × 1600. Fig. 2: complete mature frustule, oblique girdle view, pleura of epicingulum much eroded, × 1075. Fig. 3: two sibling valves, girdle view, note Crawford step on left-hand valve, × 850. Fig. 4: external view of central portion of valve, vela present in some areolae, × 9500. Fig. 5: oblique external view of central portion of valve showing marginal ridge not interrupted, superficial spines and external tube of labiate process, × 3200. Fig. 6: oblique view of same specimen as fig. 3, × 650. Fig. 7: oblique proximal view of elevation, × 4500. Fig. 8: oblique polar view of elevation showing pseudocellus, × 3750. Fig. 9: view showing linking spines and external tubes of labiate processes, × 2000.

Plate 3. *Briggera siberica* (Grunow) R. Ross & P. A. Sims. Simbirsk (now Ulyanovsk), Ulyanovsk oblast, U.S.S.R. All figures of same specimen. Fig. 1: oblique girdle view of valve, × 1350. Fig. 2: interior view of valve showing two labiate processes, one on either side of centre, × 1350. Fig. 3: girdle view of valve showing external tubes of two labiate processes, × 1250. Fig. 4: valve, oblique internal view, × 1200. Fig. 5: elevation, × 6250. Fig. 6: internal view of centre of valve showing two labiate processes, × 3000. Fig. 7: side view of valve centre, × 4250.

Plate 4. *Briggera monoligata* R. Ross & P. A. Sims. 'Singiliewsky', presumed to be Sengilei, Ulyanovsk oblast, U.S.S.R. Fig. 1: two sibling valves, girdle view, note Crawford step on right-hand one, × 1000. Fig. 2: detail of fig. 1 showing single large linking spine on elevation, × 1800. Fig. 3: portion of another specimen consisting of two sibling valves showing single large linking spine on one elevation of each valve, × 2100. Fig. 4: same specimen as fig. 1 showing large linking spine on one elevation and the small flange-like one on the other, × 1350. Fig. 5: two sibling valves with remains of girdle of parent cell, × 1250. Fig. 6: detail of fig. 5, × 2500.

Plate 5. *Briggera monoligata* R. Ross & P. A. Sims. 'Singiliewsky', presumed to be Sengilei, Ulyanovsk oblast, U.S.S.R. Fig. 1: oblique view of single valve, × 900. Fig. 2: same specimen, slightly oblique girdle view, × 900. Fig. 3: interior view of valve, × 900. Fig. 4: specimen illustrated in figs 1 & 2, slightly oblique valve view, × 650. Fig. 5: elevation and broken linking spine of same specimen, × 3000. Fig. 6: other elevation and pseudocellus of same specimen, × 2125. Fig. 7: detail of fig. 3 showing central portion of valve and two labiate processes, × 2500.

Plate 6. *Briggera capitata* (Grev.) R. Ross & P. A. Sims. Oamaru, Otago, New Zealand. Fig. 1: single valve, external valve view, × 675. Fig. 2: single valve, internal view, × 900. Fig. 3: single valve, external valve view, × 1050. Fig. 4: single valve, oblique external view, note Crawford step, × 900. Fig. 5: frustule and attached valve, × 400. Fig. 6: same specimen as fig. 1, central part of valve showing traces of vela, × 5500. Fig. 7: detail of specimen illustrated in fig. 5, × 1800. Fig. 8: elevations of two linked sibling valves, × 1800. Fig. 9: detail of valve illustrated in fig. 4 showing elevation with pseudocellus, × 1650.

Plate 7. *Briggera vemae* R. Ross & P. A. Sims. South-western Atlantic, 47° 28.7′ S, 59° 20.6′ W, 1167 m depth; Vema cruise 12, core 46, 630 cm. Fig. 1: single valve, oblique external view, × 375. Fig. 2: two linked sibling valves, girdle view, note Crawford step on lower, × 375. Fig. 3: same specimen as fig. 2, oblique view, × 375. Fig. 4: same specimen as figs 2 & 3, oblique view of central portion showing internal opening of one labiate process, × 1200. Fig. 5: same specimen as fig. 1, external valve view, × 375. Fig. 6: same specimen as fig. 2, elevations showing pseudocelli and linking spines, × 1800. Fig. 7: detail of fig. 1 showing central portion of valve, × 1450. Fig. 8: oblique proximal view of lower elevation of specimen illustrated in fig. 5, linking spines broken off, grooves between visible, × 1800. Fig. 9: upper elevation of specimen illustrated in fig. 5 with linking spines and pseudocellus, × 1800.

Plate 8. *Briggera affixa* (R. Ross) R. Ross & P. A. Sims. 'Kamichev', presumed to be Kamyshlov, Sverdlovsk oblast, U.S.S.R. Fig. 1: single valve, oblique external view, × 1275. Fig. 2: same specimen, external valve view, × 750. Fig. 3: polar portion of valve and girdle elements, × 3000. Fig. 4: detail of fig. 1 showing elevation with pseudocellus, × 2750. Fig. 5: oblique polar view of same elevation showing pattern of areolation of pseudocellus, × 3250. Fig. 6: detail of fig. 2 showing central portion of valve, × 2750.

Plate 9. *Briggera affixa* (R. Ross) R. Ross & P. A. Sims. 'Kamichev', presumed to be Kamyshlov, Sverdlovsk oblast, U.S.S.R. Fig. 1: single valve, girdle view, × 2250. Fig. 2: same valve, oblique external view, note Crawford step, × 2250. Fig. 3: whole frustule with linked sibling valve, much of girdle lost, × 675. Fig. 4: detail of fig. 3 showing tall elevations, linking spines and pseudocelli, × 1600. Fig. 5: girdle elements surrounding two sibling valves, with two elements of epicingulum and three of hypocingulum, × 925. Fig. 6: single valve, girdle view, and attached valvocopula, part of specimen illustrated in fig. 3, × 1800.

Plate 10. *Briggera ornithocephala* (Grev.) R. Ross & P. A. Sims subsp. *ornithocephala*. Oamaru, Otago, New Zealand. Fig. 1: single valve, external valve view, × 625. Fig. 2: single valve, oblique external view, note vertical row of areolae on distal face of elevation, × 850. Fig. 3: two linked sibling valves, oblique view, × 725. Fig. 4: detail of fig. 5, tips of two elevations showing linking spines and pseudocelli, × 3200. Fig. 5: two linked sibling valves with girdle bands, probably valvocopulae, of parent cell, × 600. Fig. 6: detail of fig. 5 showing probable valvocopula, × 1650. Fig. 7: same specimen as fig. 5, oblique view, × 1150. Fig. 8: detail of fig. 3, internal view of central part of valve, × 1550.

Plate 11. *Briggera ornithocephala* subsp. *atlantica* R. Ross & P. A. Sims. Figs 1–3, 5, 6: south-western Atlantic, 51° 08′ S, 54° 22′ W, 1525 m depth; Vema cruise 17, core 107, 120 cm. Figs 4, 7: south-western Atlantic, 53° 01′ S, 52° 52′ W, 2880 m depth; Vema cruise 18, core 104, 330 cm. Fig. 1: single valve, oblique external view, × 1125. Fig. 2: same valve, external valve view, × 1325. Fig. 3: same valve, oblique polar view, note vertical row of areolae on distal face of elevation, × 925. Fig. 4: two sibling valves, slightly oblique girdle view, × 550. Fig. 5: detail of fig. 3 showing pseudocellus and linking spines, × 3000. Fig. 6: same specimen as fig. 1, central part of valve showing superficial granules, × 5750. Fig. 7: detail of fig. 4 showing one valve, × 775.

Plate 12. *Briggera ornithocephala* subsp. *atlantica* R. Ross & P. A. Sims. Figs 1, 4, 6, 7: south-western Atlantic, 53° 01′ S, 52° 52′ W, 2880 m depth; Vema cruise 18, core 104, 330 cm. Figs 2, 3, 5: south-western Atlantic 51° 08′ S, 54° 22′ W, 1525 m depth; Vema cruise 17, core 107, 120 cm. Fig. 1: single valve, external valve view, × 725. Fig. 2: single valve, girdle view, × 850. Fig. 3: same valve, oblique internal view, × 600. Fig. 4: same valve as fig. 1, oblique external view, note Crawford step, × 700. Fig. 5: same specimen as fig. 2, elevation showing linking spines and pseudocellus, × 2000. Fig. 6: detail of fig. 1, central part of valve, × 3750. Fig. 7: same valve as figs 1 & 4, oblique view showing pseudocellus, note no vertical row of areolae on distal side of elevation, × 1550.

Plate 13. *Briggera bonei* R. Ross & P. A. Sims. Figs 1–5: south-western Atlantic, 51° 08′ S, 54° 22′ W, 1525 m depth; Vema cruise 17, core 107, 120 cm. Figs 6–8: south-western Atlantic, 53° 01′ S, 52° 52′ W, 2880 m depth; Vema cruise 18, core 104, 330 cm. Fig. 1: single valve, oblique external view, note Crawford step, × 575. Fig. 2: same valve, external valve view, × 625. Fig. 3: polar view of part of same valve showing

pseudocellus and linking spines, × 1500. Fig. 4: detail of same valve showing areolation, some areolae with two small pegs on their margins, × 1875. Fig. 5: proximal side of elevation of same valve, × 1675. Fig. 6: pair of small sibling valves with single sulcus, two girdle elements present, × 600. Fig. 7: detail of fig. 6 showing pseudocelli and linking spines, × 1875. Fig. 8: same specimen as fig. 6 showing girdle elements, × 1150.

Plate 14. Figs 1–4: *Briggera novocastrensis* (R. Ross) R. Ross & P. A. Sims. Indian Ocean, 10° 25′ S, 63° 15′ E, 3115 m depth; dredge sample, Dodo-123-D1. Fig. 1: single valve, polar oblique external view, × 675. Fig. 2: same valve, oblique external view, × 725. Fig. 3: detail of same specimen showing linking spines and divided pseudocellus, × 1650. Fig. 4: proximal side of elevation of same valve showing linking spines, × 2150. Figs 5–8: *Briggera haitensis* (R. Ross) R. Ross & P. A. Sims. Conset, Barbados. Fig. 5: pair of sibling valves, oblique view, × 650. Fig. 6: detail of same specimen showing divided pseudocelli, × 1500. Fig. 7: detail of fig. 8 showing linking spines × 1650. Fig. 8: oblique polar view of specimen in fig. 5, × 825.

Plate 15. *Briggera paratethyos* R. Ross & P. A. Sims. Pouzdřany (formerly Pausram), Czechoslovakia. Fig. 1: single valve, external valve view, × 750. Fig. 2: single valve, oblique view, × 900. Fig. 3: single valve, girdle view, × 1225. Fig. 4: detail of fig. 1 showing tip of elevation with pseudocellus, × 2400. Fig. 5: detail of fig. 1 showing areolation and sulcus, × 2400. Fig. 6: same specimen as fig. 2, polar view showing pseudocellus and vertical row of small areolae on distal face of elevation, × 1300.

Plate 16. *Briggera* sp. I. Exposure XI (14), Til'tim, Tyumen'sk oblast, U.S.S.R. All figures of same specimen. Fig. 1: single valve, oblique external view, × 950. Fig. 2: detail of fig. 3 showing pseudocellus and broken linking spines, × 3400. Fig. 3: external valve view, × 950. Fig. 4: oblique polar view showing pseudocellus and vertical row of areolae on distal face of elevation, × 2100. Fig. 5: oblique view, detail showing elevation with pseudocellus, broken linking spines and sulcus, × 2400. Fig. 6: detail of fig. 3 showing areolation, × 4750. Fig. 7: oblique proximal view of elevation showing broken linking spines and grooves between widening below, × 3600.

Plate 17. *Dicladiopsis alta* R. Ross & P. A. Sims. 'Kamichev', presumed to be Kamyshlov, Sverdlovsk oblast, U.S.S.R. Fig. 1: single valve, girdle view, × 1000. Fig. 2: single valve, oblique external view, × 825. Fig. 3: detail of fig. 1, × 1450. Fig. 4: same specimen as fig. 2, mantle and lower part of valve, × 1450. Fig. 5: detail of fig. 1 showing elevations with pseudocelli, both partly broken away, and one linking spine with broken bases of others, × 1900. Fig. 6: detail of fig. 2 showing elevations with pseudocelli broken away, × 1650. Fig. 7: detail of specimen illustrated in fig. 1 showing vertical row of areolae on distal face of elevation, × 2100. Fig. 8: detail of fig. 2 showing vertical row of areolae on distal face of elevation, × 2650.

Plate 18. *Dicladiopsis erecta* R. Ross & P. A. Sims. 'Kamichev', presumed to be Kamyshlov, Sverdlovsk oblast, U.S.S.R. Fig. 1: single valve, oblique external view, × 1450. Fig. 2: single valve, oblique polar view showing vertical row of areolae on distal face of elevation, × 1500. Fig. 3: tip of elevation of specimen illustrated in fig. 1 showing pseudocellus, broken linking spines and vertical row of areolae on distal face of elevation, × 3750. Fig. 4: presumed valve without linking spines, oblique external view, × 900. Fig. 5: same specimen as fig. 4 showing vertical row of areolae on distal face of elevation, × 3000. Fig. 6: detail of specimen illustrated in fig. 7 showing mantle and vertical row of areolae on distal face of elevation, × 2800. Fig 7: single valve, oblique girdle view, × 950.

Plate 19. *Dicladiopsis* sp. I. 'Kamichev', presumed to be Kamyshlov, Serdlovsk oblast, U.S.S.R. All figures of same specimen. Fig. 1: whole frustule, girdle view, × 950. Fig. 2: oblique view of valve with linking spines, × 1950. Fig. 3: oblique polar girdle view, × 775. Fig. 4: oblique polar view of girdle band and mantle of valve with linking spines, × 1900. Fig. 5: oblique polar view of valve with linking spines, × 1750. Fig. 6: elevation of valve with linking spines showing pseudocellus, flat summit and broken linking spine, × 3800. Fig. 7: elevation of valve without linking spines showing pseudocellus and rounded summit, × 3800.

Plate 20. *Strelnikovia antiqua* (Streln.) R. Ross & P. A. Sims. Core 82, near Ust'-Man'ya, Tyumen'sk oblast, U.S.S.R. All figures of same specimen. Fig. 1: whole frustule and attached valve, oblique girdle view, × 500. Fig. 2: oblique girdle view showing valve interior, × 450. Fig. 3: girdle view, × 550. Fig. 4: apices of two sibling valves showing pseudocelli and linking spines, with rotae in areolae of pseudocelli, × 3750. Fig. 5: oblique view of central part of valve, × 1700. Fig. 6: oblique view of apical part of valve showing pseudocellus, linking spines and marginal ridge, × 3000.

Plate 21. *Strelnikovia antiqua* (Streln.) R. Ross & P. A. Sims. Core 82, near Ust'-Man'ya, Tyumen'sk

oblast, U.S.S.R. Fig. 1: oblique external view of centre of valve showing hollow spines or occluded processes, × 1900. Fig. 2: oblique internal view of centre of valve showing one labiate process close to each margin, × 1800. Fig. 3: portion of specimen illustrated in pl. 20 showing girdle elements, × 1600. Fig. 4: detail of fig. 3, × 4500. Fig. 5: oblique external polar view of valve showing pseudocellus and broken linking spines, × 3250. Fig. 6: detail of central portion of valve, external view, showing areolae with rotae, × 20,000. Fig. 7: internal view of apex of valve, × 3250.

Plate 22. *Strelnikovia tumida* R. Ross & P. A. Sims. Core 82, near Ust'-Man'ya, Tyumen'sk oblast, U.S.S.R. All figures of same specimen. Fig. 1: oblique external view of valve, × 1100. Fig. 2: oblique external view of valve, × 750. Fig. 3: external valve view, × 700. Fig. 4: oblique external view of apex of valve showing pseudocellus and broken linking spines, × 2500. Fig. 5: oblique external view of elevation showing two intact linking spines, × 2500. Fig. 6: oblique external view of apex showing pseudocellus and elevation with two intact linking spines, × 2000. Fig. 7: external view of central part of valve, × 4000.

Plate 23. *Strelnikovia auliscoformis* (Streln.) R. Ross & P. A. Sims. Exposure XI (14), Til'tim, Tyumen'sk oblast, U.S.S.R. All figures of same specimen. Fig. 1: oblique view of two sibling valves, × 700. Fig. 2: internal view of one valve, × 900. Fig. 3: elevations showing pseudocelli, × 1650. Fig. 4: elevations showing linking spines, × 1900. Fig. 5: detail of surface in external view, × 8500. Fig. 6: centre of valve, internal view, × 3400. Fig. 7: internal view of elevation, × 2800.

Plate 24. *Strelnikovia inclinata* R. Ross & P. A. Sims. Exposure XI (14), Til'tim, Tyumen'sk oblast, U.S.S.R. All figures of same specimen. Fig. 1: oblique external view of valve, × 1000. Fig. 2: external valve view, × 950. Fig. 3: oblique polar external view of valve, × 900. Fig. 4: external view of centre of valve, × 3500. Fig. 5: elevation showing eroded bases of linking spines, × 2700. Fig. 6: other elevation in oblique polar view, × 2000. Fig. 7: vertical view of elevation shown in fig. 5, × 3300.

Plate 25. *Strelnikovia reniformis* R. Ross & P. A. Sims. Core 82, near Ust'-Man'ya, Tyumen'sk oblast, U.S.S.R. All figures of same specimen. Fig. 1: oblique polar external view of valve, × 925. Fig. 2: external valve view, × 925. Fig. 3: external view of margin of valve, × 3250. Fig. 4: external view of centre of valve, × 2800. Fig. 5: vertical external view of elevation showing eroded bases of linking spines, × 2750. Fig. 6: oblique polar view of other elevation showing pseudocellus, × 1800.

Plate 26. *Strelnikovia incerta* R. Ross & P. A. Sims. 'Kamichev', presumed to be Kamyshlov, Sverdlovsk oblast, U.S.S.R. Fig. 1: valve view, × 675. Fig. 2: same specimen, oblique polar view, × 775. Fig 3: same specimen, oblique side view of elevation showing broken off presumed linking spines, × 3300. Fig. 4: same specimen, oblique polar view of elevation showing pseudocellus, × 4000. Fig. 5: same specimen, external view of valve centre; the radially elongated holes are the external openings of the labiate processes, × 2800. Fig. 6: detail of fig. 5 showing external openings of two labiate processes at the top and areolae with remains of vela, × 8000. Fig. 7: oblique internal view of valve, × 1000. Fig. 8: detail of fig. 7 showing central area of valve with internal openings of labiate processes, × 5000.

Plate 27. *Strelnikovia* sp. I. Core 82, near Ust'-Man'ya, Tyumen'sk oblast, U.S.S.R. All figures of same specimen. Fig. 1: girdle view of hypovalve and girdle elements of epivalve, × 600. Fig. 2: oblique view, × 800. Fig. 3: valve and part of girdle showing remains of a much eroded girdle band of epivalve along free edge of well preserved band, × 1100. Fig. 4: elevation showing a few intact linking spines, × 3600. Fig. 5: valve surface near centre showing very small sparse areolae, × 10,000. Fig. 6: oblique view of elevation illustrated in fig. 4 showing linking spines and pseudocellus, × 3750. Fig. 7: part of other elevation showing broken bases of linking spines and areolae of pseudocellus with volae and rotae, × 13,000. Fig. 8: part of girdle, × 2500.

Plate 28. *Keratophora nitida* Pant. 'Kamichev', presumed to be Kamyshlov, Sverdlovsk oblast, U.S.S.R. Fig. 1: oblique view of two sibling valves, × 800. Fig. 2: detail of fig. 1 showing tips of elevations with pseudocelli and interlocking linking spines, × 2300. Fig. 3: tip of elevation showing broken linking spines and extension of pseudocellus onto summit of elevation, × 3800. Fig. 4: detail of surface of valve showing vela, × 12,500. Fig. 5: interior view of valve, × 800. Fig. 6: two sibling valves surrounded by portion of girdle of parent cell, × 1000. Fig. 7: detail of fig. 6, × 2250.

Plate 29. Figs 1–7: *Keratophora nitida* Pant. 'Kamichev', presumed to be Kamyshlov, Sverdlovsk oblast, U.S.S.R. Fig. 1: oblique external view of valve with elevations inserted further from centre than normal and constricted below tips, × 750. Fig. 2: same specimen, external valve view, × 850. Fig. 3: oblique external view of another specimen with elevations inserted further from centre than normal, × 750. Fig. 4: oblique external view of valve with very tall, only slightly sinuous elevations, presumed end cell, × 800. Fig. 5: detail of fig. 4 showing tip of elevation with poorly developed linking spines, × 3800. Fig. 6:

girdle view of another presumed end cell, × 700. Fig. 7: two sibling valves, oblique view, upper with marginal ridge, lower without, × 450. Fig. 8: *Hemiaulus* sp. 'Kamichev', presumed to be Kamyshlov, Sverdlovsk oblast, U.S.S.R. Spore (*Keratophora nuda* Meister) with attached vegetative valve, × 700.

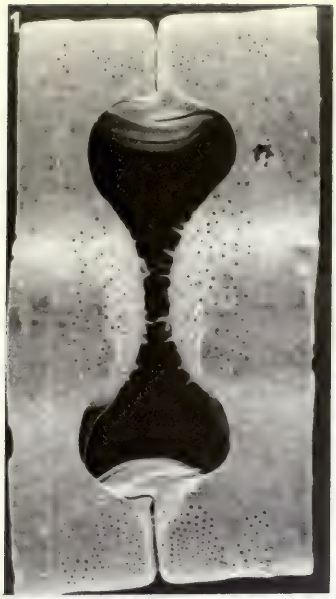
Plate 30. Fig. 1: Simbirsk (now Ulyanovsk), Ulyanovsk oblast, U.S.S.R.; presumed end cell of *Briggera includens* (Grunow) R. Ross & P. A. Sims, × 900. Fig. 2: 'Carlovo', U.S.S.R.; presumed end cell of *Briggera includens* × 550. Fig. 3: exposure XI (14), Til'tim, Tyumen'sk oblast, U.S.S.R.; *Biddulphia* sp., × 550. Fig. 4: core 82, near Ust'-Man'ya, Tyumen'sk oblast, U.S.S.R.; *Biddulphia* sp., × 650. Fig. 5: exposure XI (14), Til'tim, Tyumen'sk oblast, U.S.S.R.; ? genus, × 700. Fig. 6: exposure XI (14), Til'tim, Tyumen'sk oblast, U.S.S.R.; ? genus, × 750. Fig. 7: core 82, near Ust'-Man'ya, Tyumen'sk oblast, U.S.S.R.; ? genus, × 1100. Fig. 8: same specimen as fig. 7, × 1100.

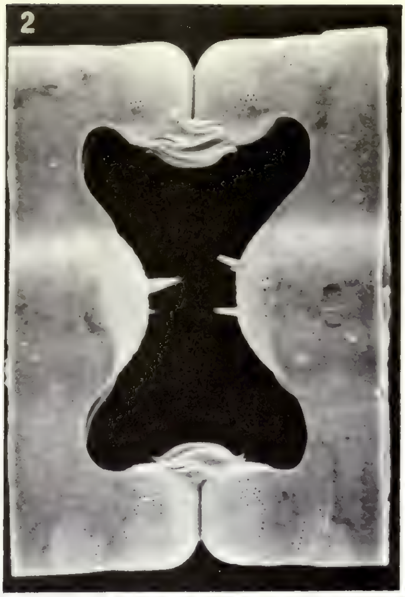
Plate 31. Fig. 1: *Briggera morenoensis* R. Ross & P. A. Sims. Holotype BM 81100: Moreno, Panoche, California, U.S.A.; apical axis 70 μm. Fig. 2: *Briggera monoligata* R. Ross & P. A. Sims. Holotype BM 81102: 'Singiliewsky', presumed to be Sengilei, Ulyanovsk oblast, U.S.S.R.; apical axis 73 μm. Fig. 3: *Briggera vemae* R. Ross & P. A. Sims. Holotype BM 81103: South-western Atlantic, 47° 28.7′ S, 59° 20.6′ W, 1167 m depth; Vema cruise 12, core 46, 630 cm; apical axis 155 μm. Fig. 4: *Briggera robusta* R. Ross & P. A. Sims. Holotype BM Adams TS 693: Kuznetsk, Penza oblast, U.S.S.R.; apical axis 140 μm. Fig. 5a, b: *Briggera caverna* (Brun) R. Ross & P. A. Sims. Syntype G coll. Brun 3074: Kuznetsk, Penza oblast, U.S.S.R.; apical axis 72 μm. Specimen taken at two focal levels a) to show central area and valve outline and b) to show centrally positioned linking spines at the summit of broken elevations. Figs 6, 7: *Briggera ornithocephala* subsp. *atlantica* R. Ross & P. A. Sims. BM 81105: South-western Atlantic, 53° 01′ S, 52° 52′ W, 2880 m depth; Vema cruise 18, core 104, 330 cm. Fig. 6: holotype, two linked valves; apical axis 95 μm. Fig. 7: single valve; apical axis 60 μm. Fig. 8: *Briggera bonei* R. Ross & P. A. Sims. Holotype BM 78447: south-western Atlantic, 51° 08′ S, 54° 22′ W, 1525 m depth; Vema cruise 17, core 107, 120 cm; apical axis 48 μm. Fig. 9: *Briggera haitensis* (R. Ross) R. Ross & P. A. Sims. Holotype BM 38251: Jérémie, Haiti; apical axis 54 μm. Fig. 10: *Briggera novocastrensis* (R. Ross) R. Ross & P. A. Sims. Holotype BM 41187: Newcastle, Barbados; apical axis 47 μm.

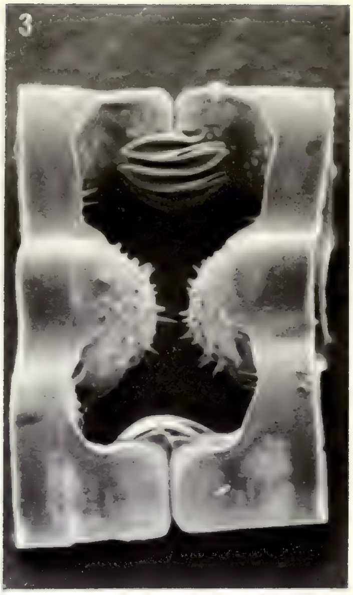
Plate 32. Figs 1, 2: *Briggera paratethyos* R. Ross & P. A. Sims. BM 81109: Pouzdřany, Czechoslovakia. Fig. 1: holotype; apical axis 63 μm. Fig. 2: specimen mounted displaying valve face. Focal level at summit of elevations. Elevations 26 μm broad. Fig. 3a, b, c: *Dicladiopsis barbadensis* (Grev.) De Toni. Holotype BM 3416: Cambridge Estate, Barbados; frustule 130 μm long, 45 μm wide at girdle. Fig. 4: *Dicladiopsis alta* R. Ross & P. A. Sims. Holotype BM 65772: 'Kamischev', presumed to be Kamyshlov, Sverdlovsk oblast, U.S.S.R.; apical axis 30 μm. Figs 5, 6, 7: *Dicladiopsis erecta* R. Ross & P. A. Sims. Fig. 5: holotype BM coll. Adams TS 747: 'Kamischev', presumed to be Kamyshlov, Sverdlovsk oblast, U.S.S.R.; two linked valves, apical axis 70 μm. Figs 6, 7: BM 81111: 'Kamischev', presumed to be Kamyshlov, Sverdlovsk oblast, U.S.S.R.; apical axis of both specimens 30 μm. Fig. 8, 9: *Dicladiopsis perlonga* (Pantocsek) R. Ross & P. A. Sims. Fig. 8: BM 74799: Kuznetsk, Penza oblast, U.S.S.R.; apical axis 73 μm. Fig. 9: BM 81112: Rostov, U.S.S.R.; apical axis 53 μm.

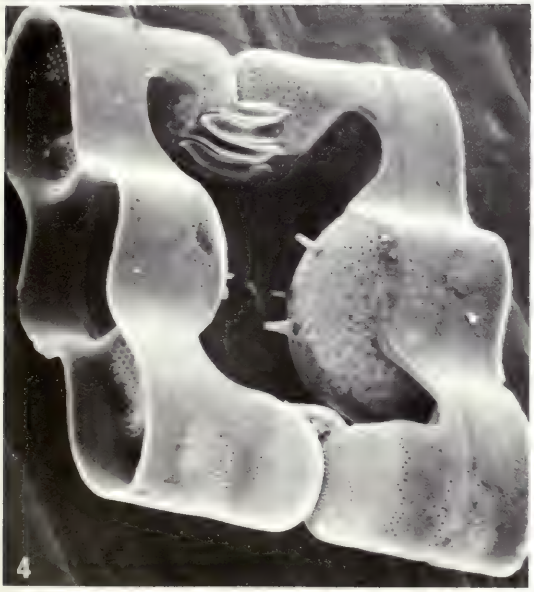
Plate 33. Fig. 1: *Strelnikovia antiqua* (Streln.) R. Ross & P. A. Sims BM 81115: core 82, near Ust'-Man'ya, Tyumen'sk oblast, U.S.S.R.; apical axis 127 μm. Fig. 2: *Strelnikovia tumida* R. Ross & P. A. Sims. Holotype BM 81118: core 82, near Ust'-Man'ya, Tyumen'sk oblast, U.S.S.R.; apical axis 102 μm. Fig. 3: *Strelnikovia inclinata* R. Ross & P. A. Sims. Holotype BM 81120: exposure XI (14), near Til'tim, Tyumen'sk oblast, U.S.S.R.; apical axis 85 μm. Fig. 4: *Strelnikovia reniformis* R. Ross & P. A. Sims. Holotype BM 81121: exposure XI (14), near Til'tim, Tyumen'sk oblast, U.S.S.R.; apical axis 65 μm. Fig. 5: *Strelnikovia incerta* R. Ross & P. A. Sims. Holotype BM 65764a: 'Kamischev', presumed to be Kamyshlov, Sverdlovsk oblast, U.S.S.R.; apical axis 122 μm. Figs 6, 7: *Thaumatonema barbadense* Grev. Fig. 6: holotype BM 2853: Cambridge, Barbados; two linked valves, apical axis 83 μm. Fig. 7: photograph Brigger coll. CAS: Joe's River, Barbados. Valve face. Figs 8, 9: *Thaumatonema costatum* Grev. Fig. 8: holotype BM 3419: Cambridge, Barbados; valve 48 μm diameter. Fig. 9: CAS coll. Brigger 43151(4): D.S.D.P., Leg. 1, Site 6, core 4, Bermuda Rise; two linked valves 122 μm long.

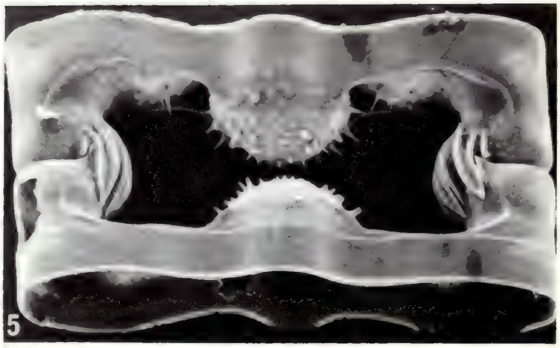
PLATE 1

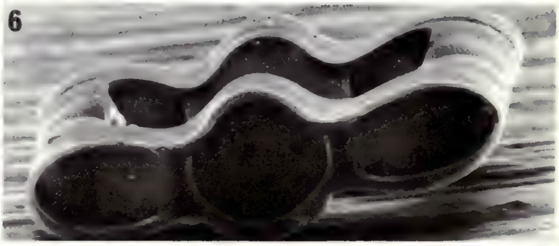


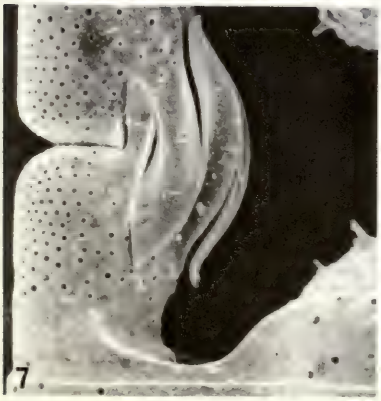


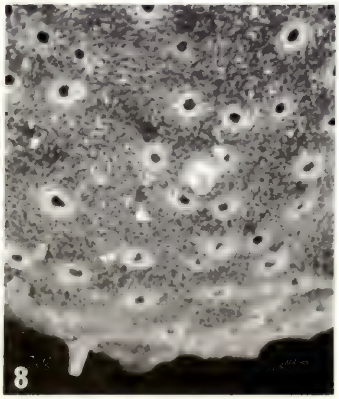


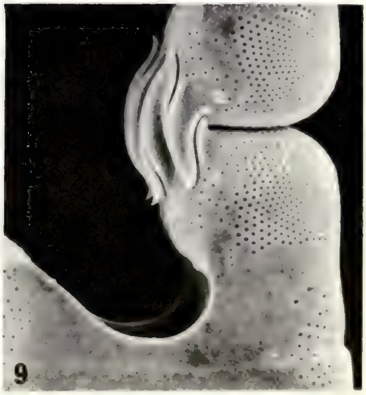


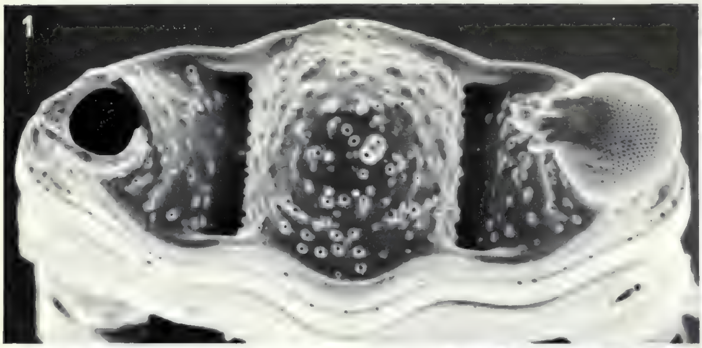








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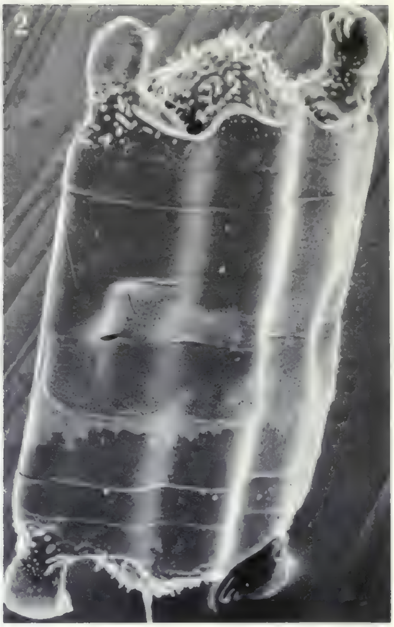
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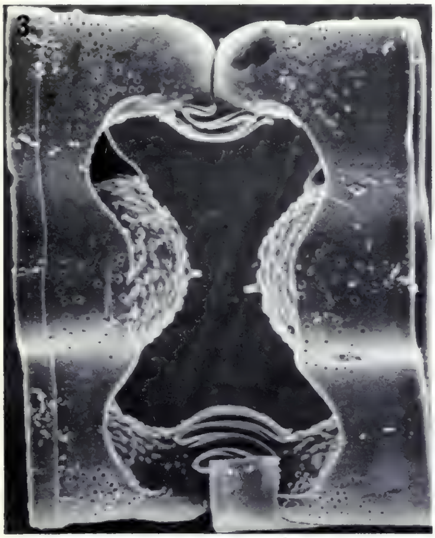
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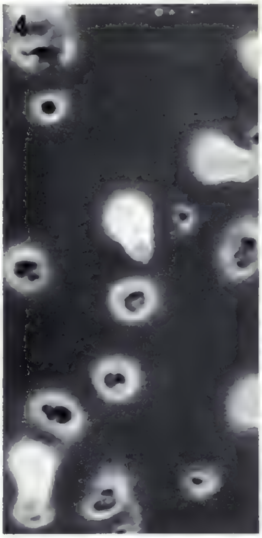
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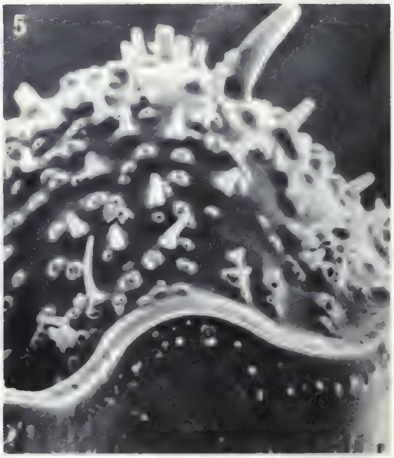
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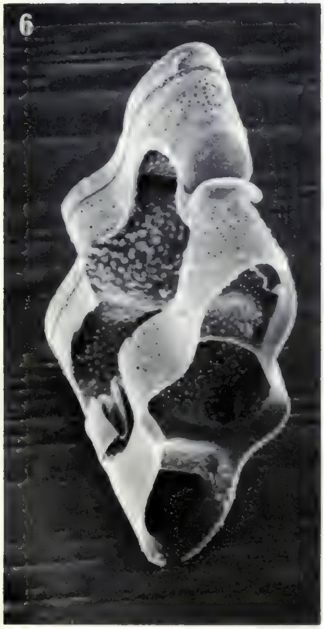
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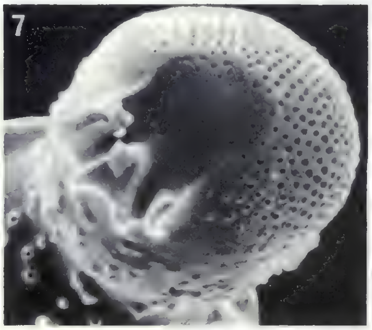
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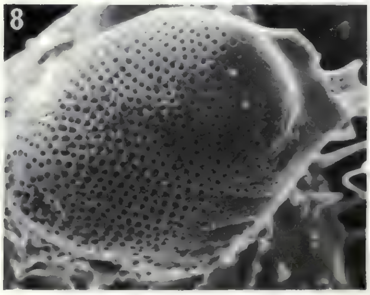
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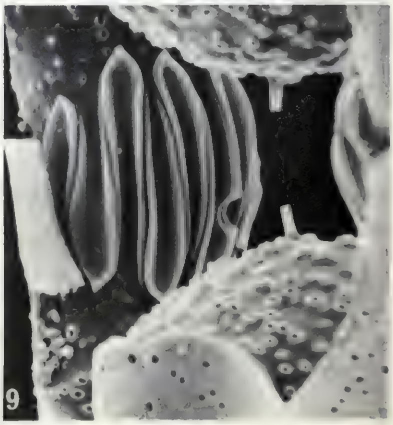
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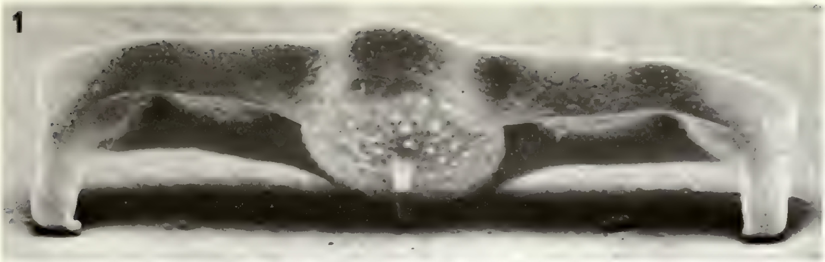

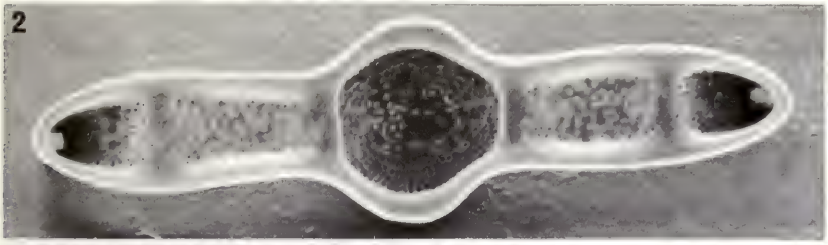

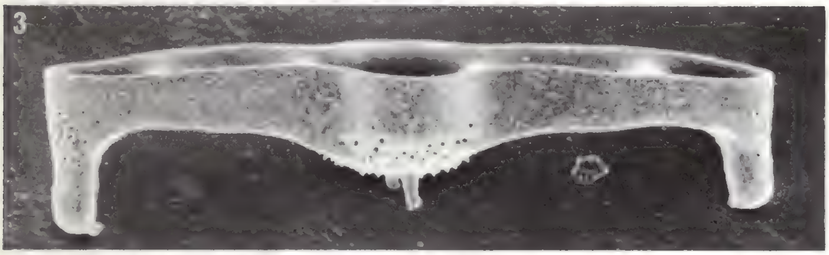

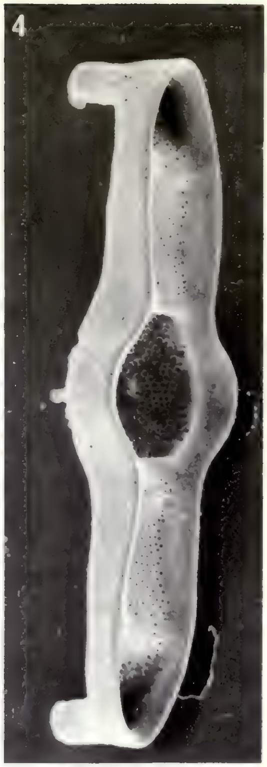

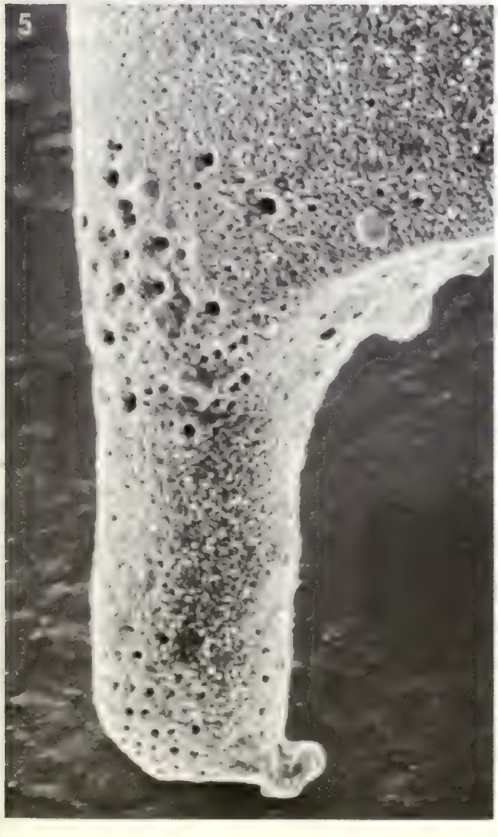

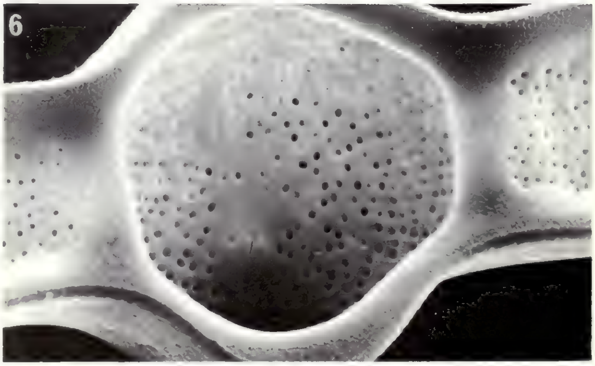

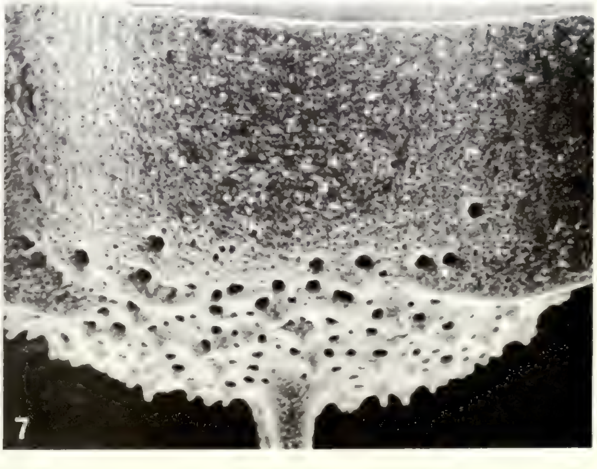

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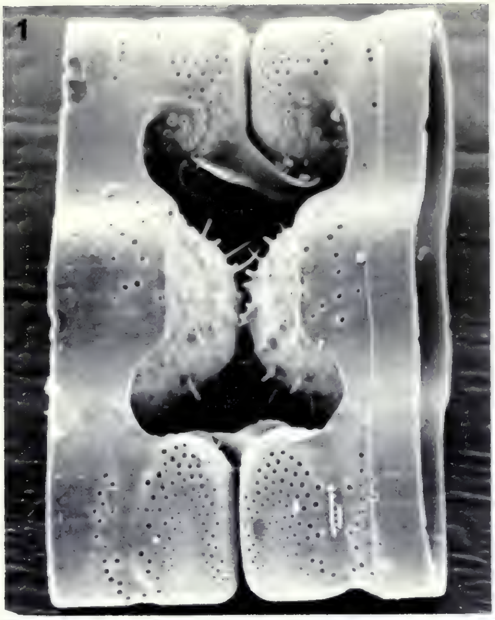
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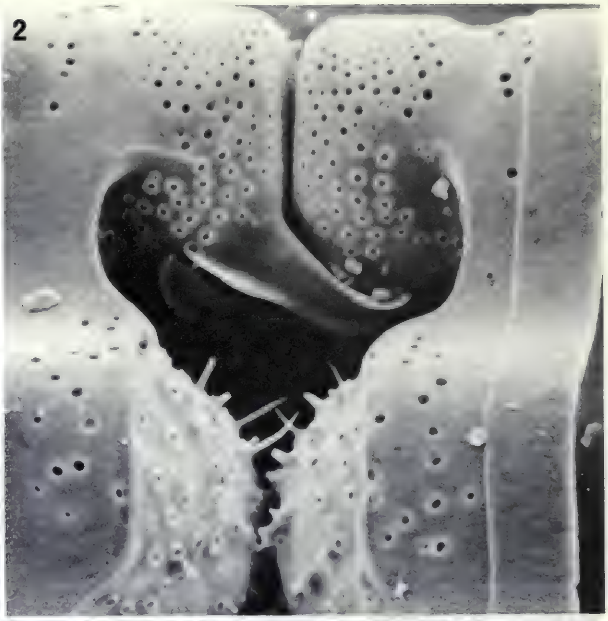
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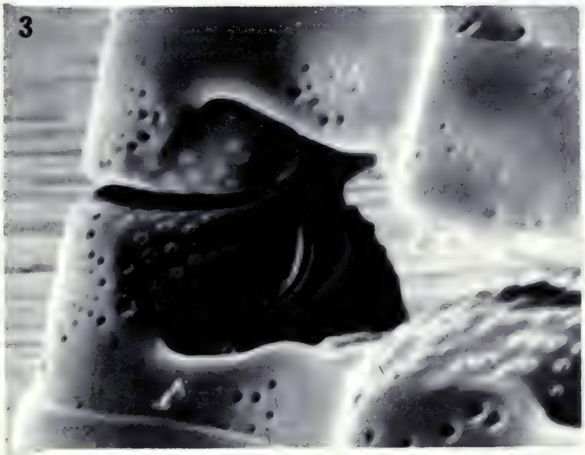
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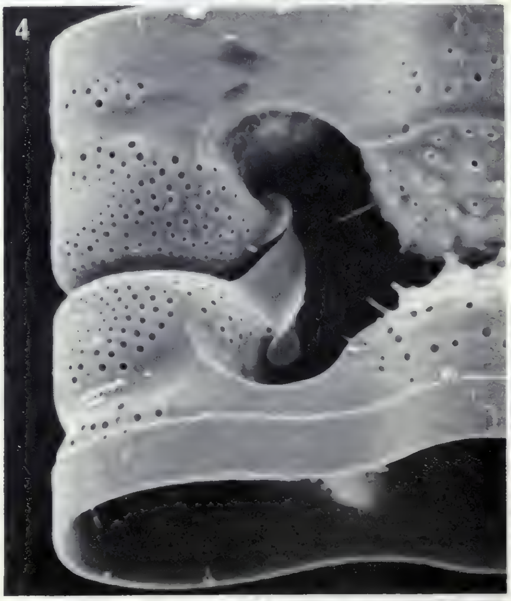
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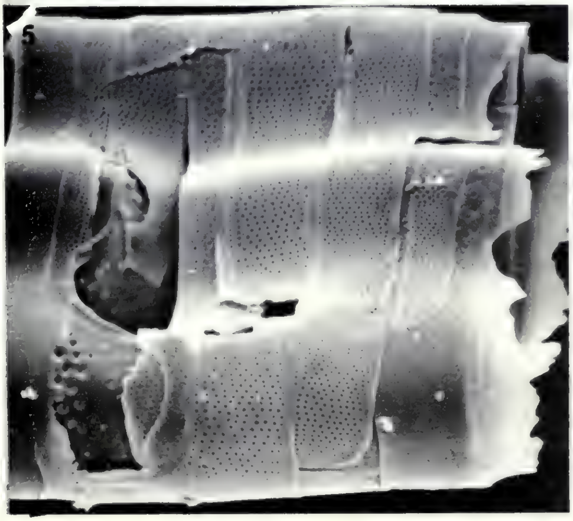
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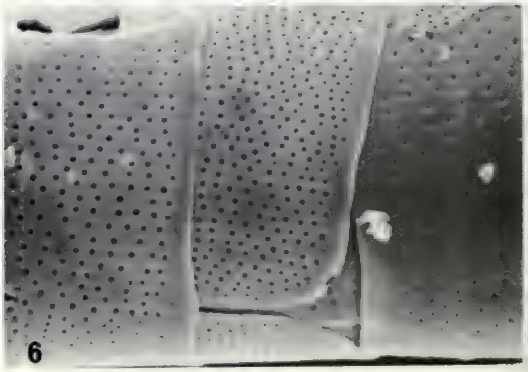
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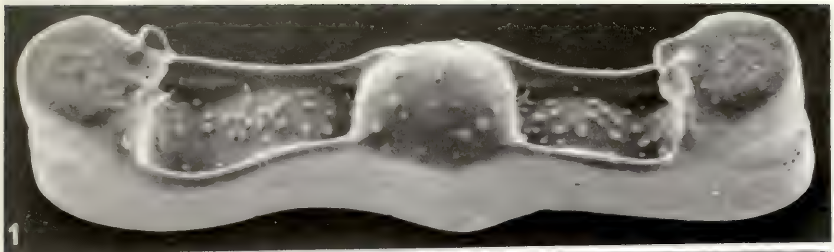

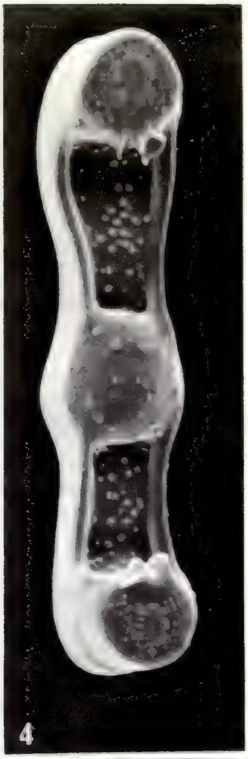

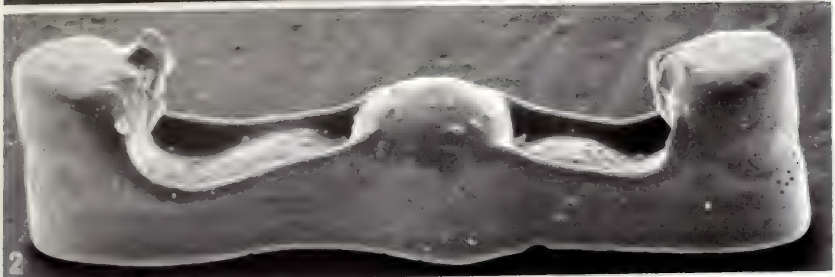

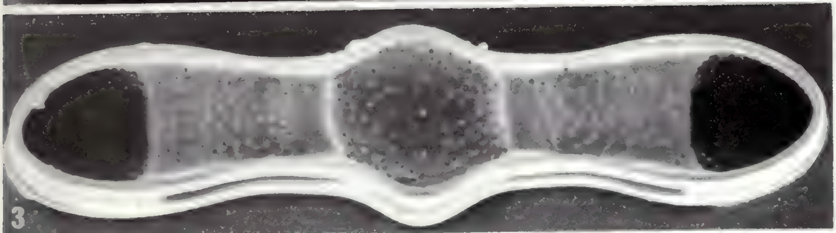

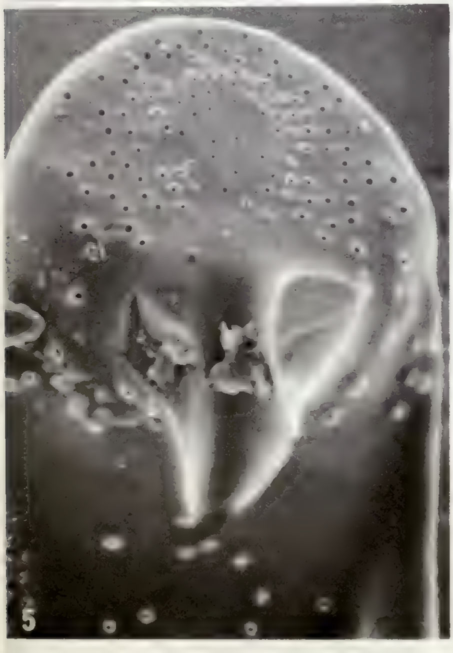

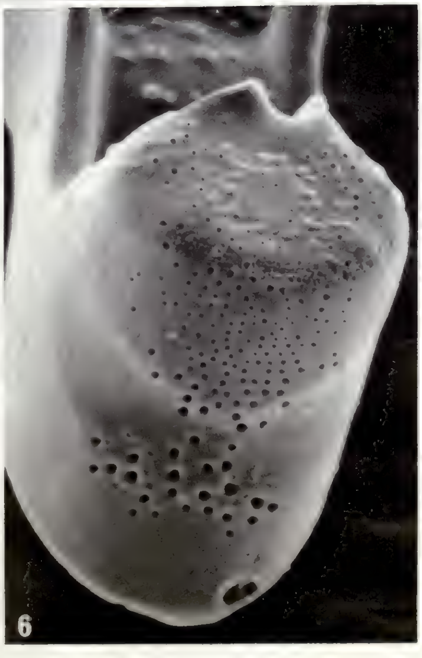

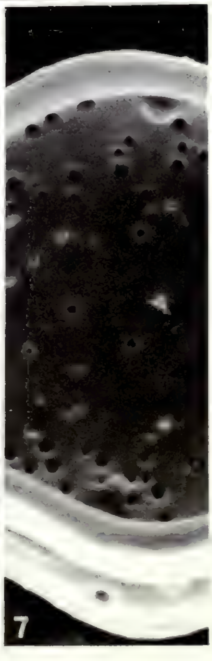

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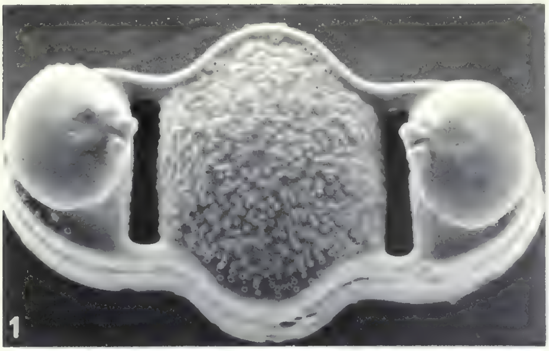
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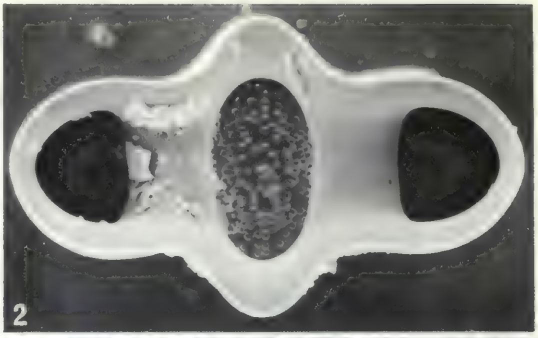
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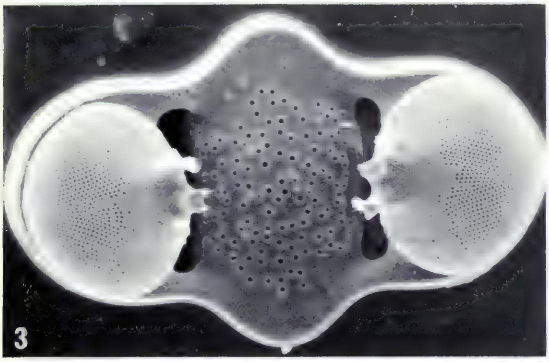
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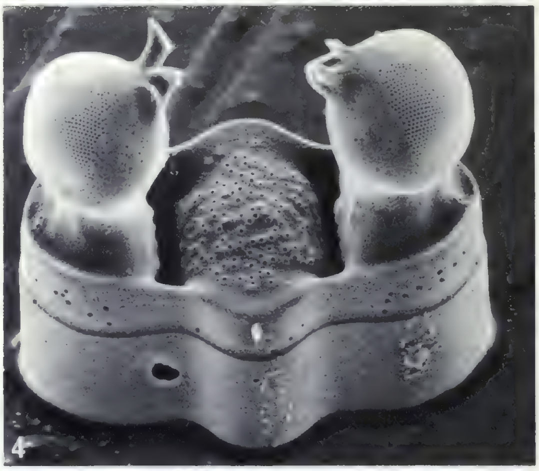
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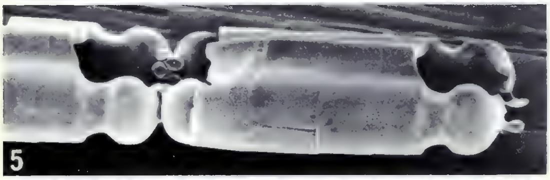
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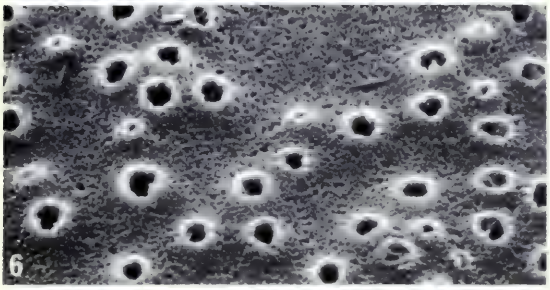
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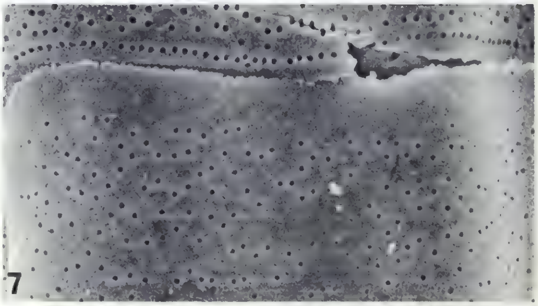
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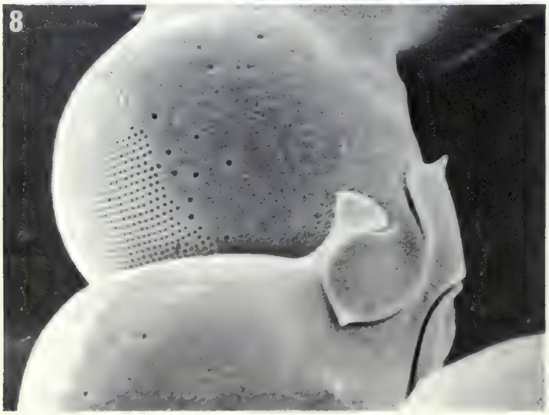
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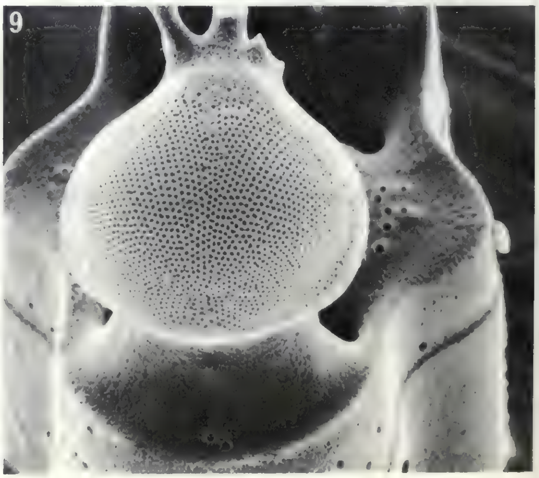
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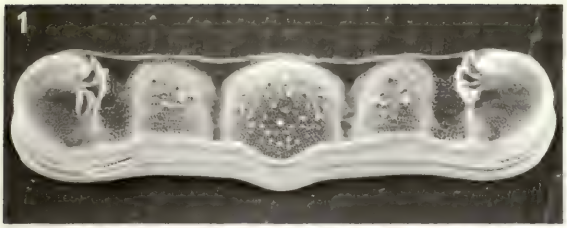
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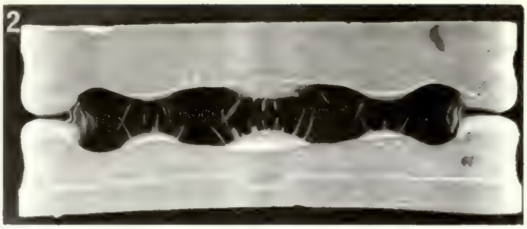
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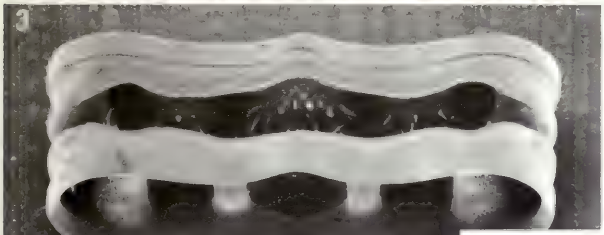
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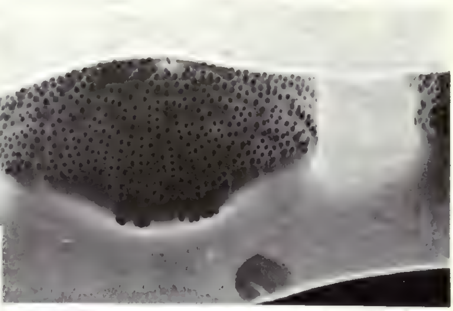
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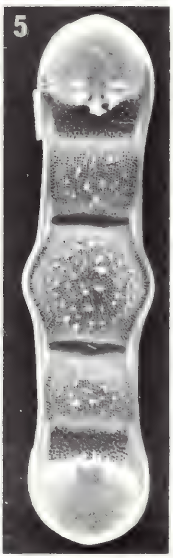
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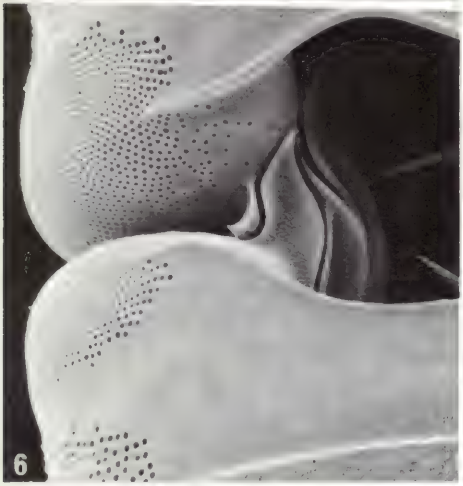
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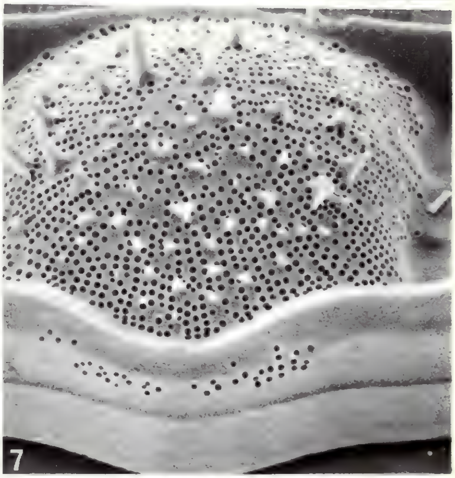
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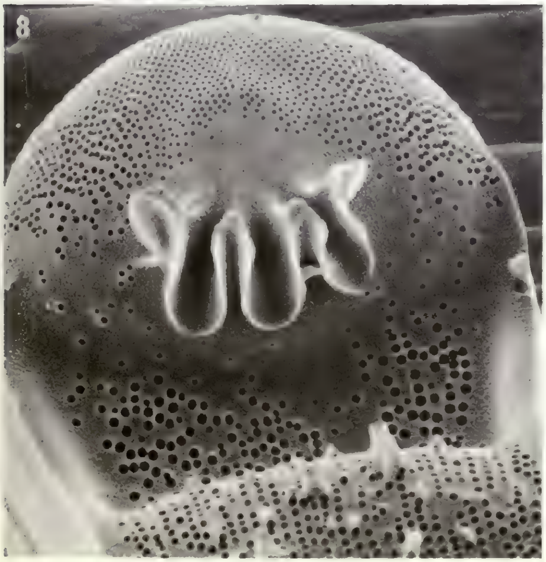
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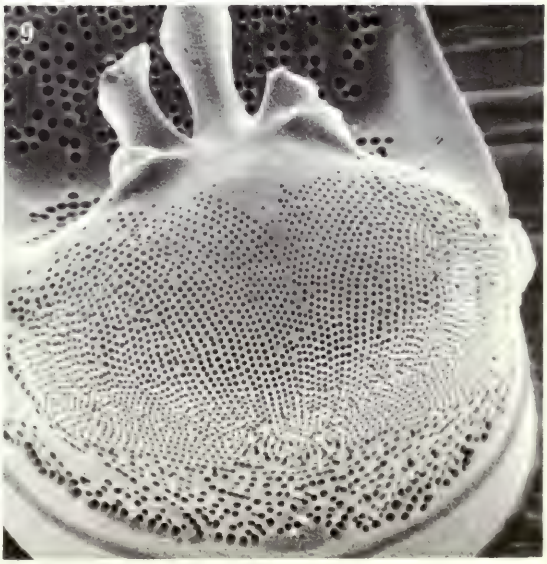
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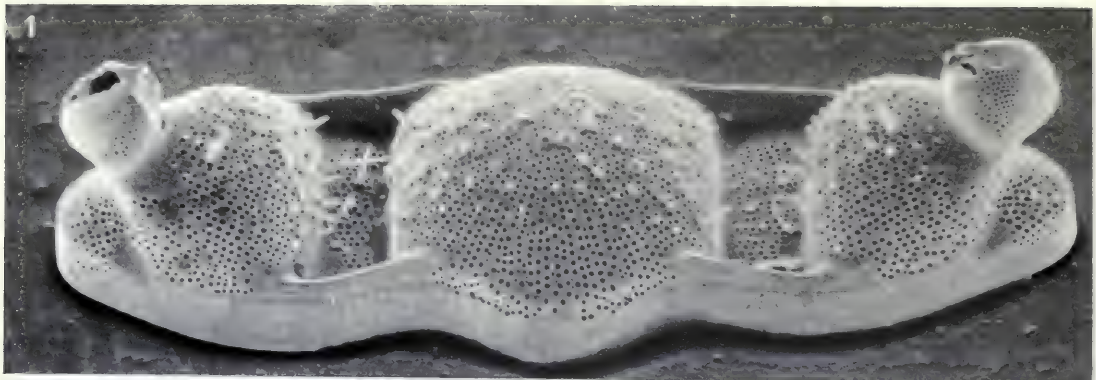
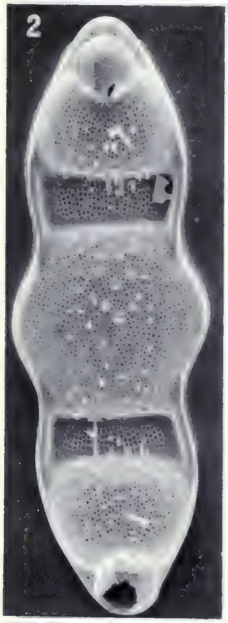
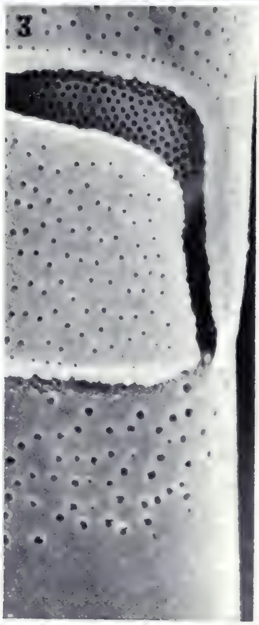
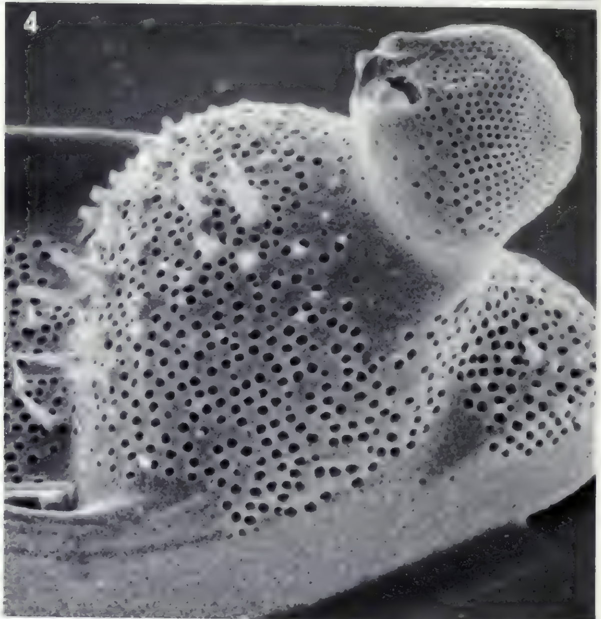
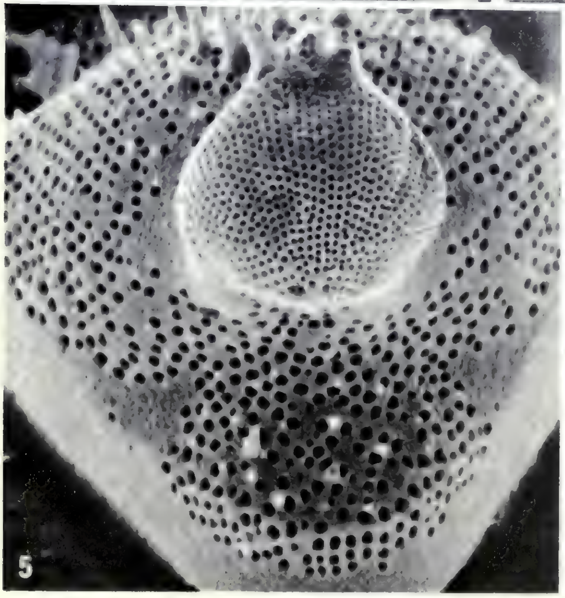
PLATE 8

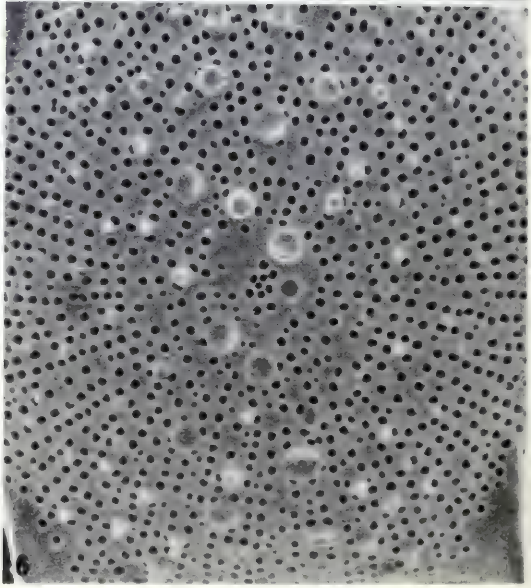


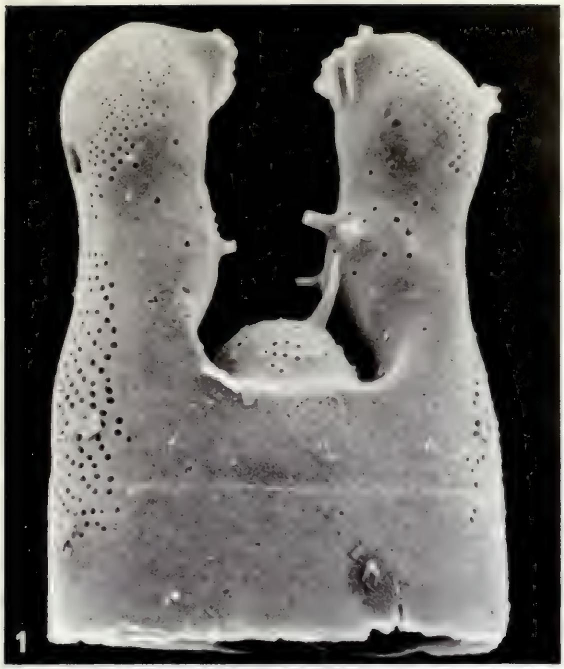








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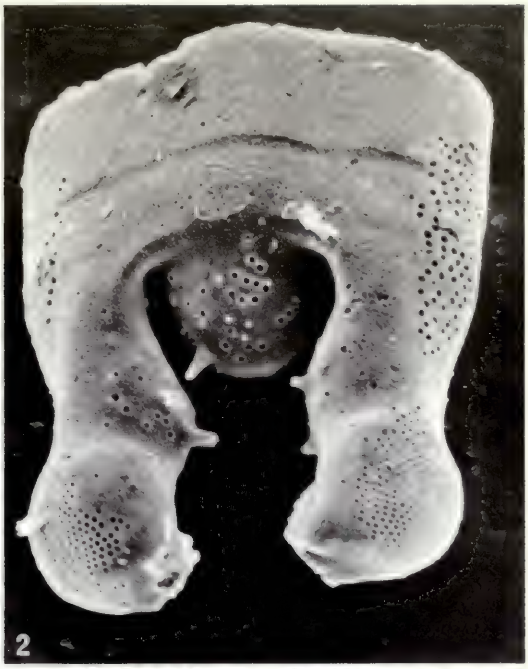
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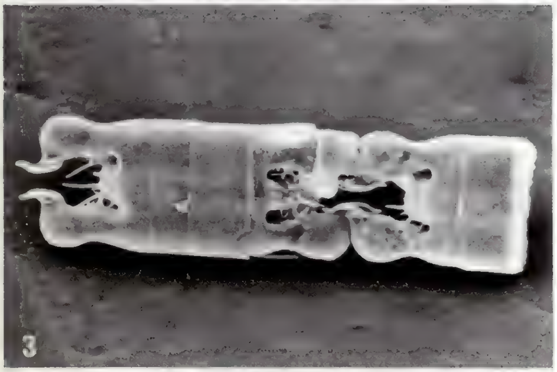
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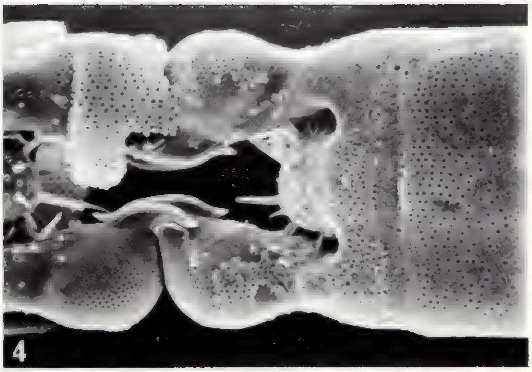
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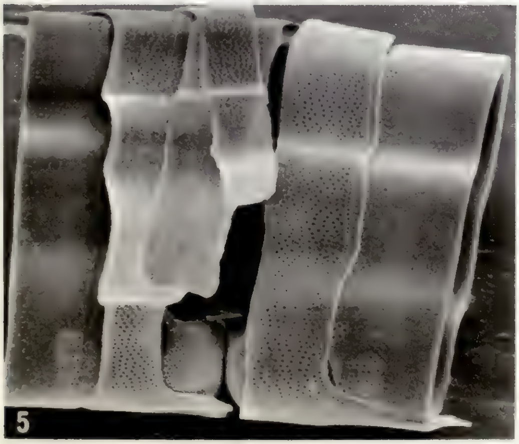
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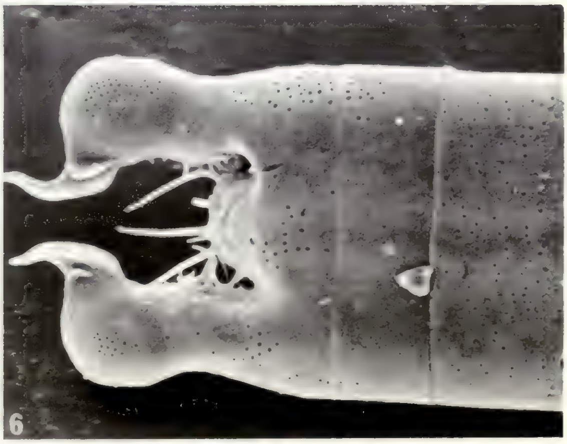
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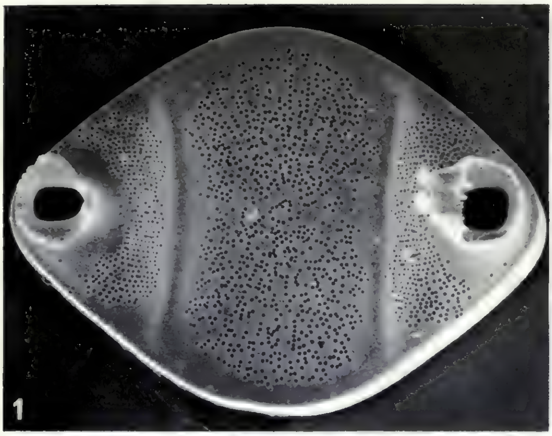
PLATE 10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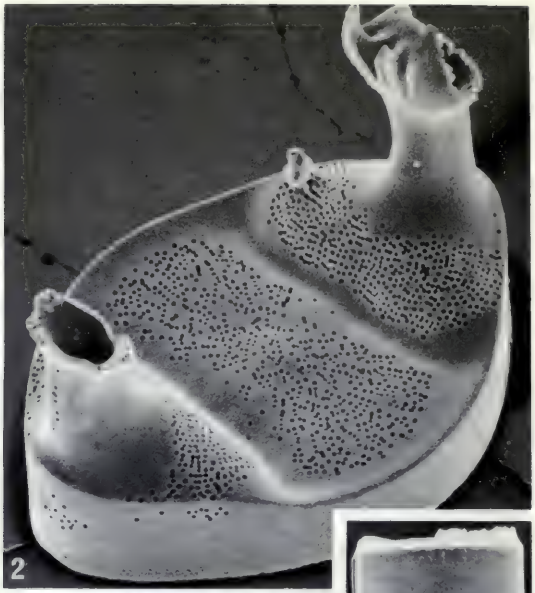
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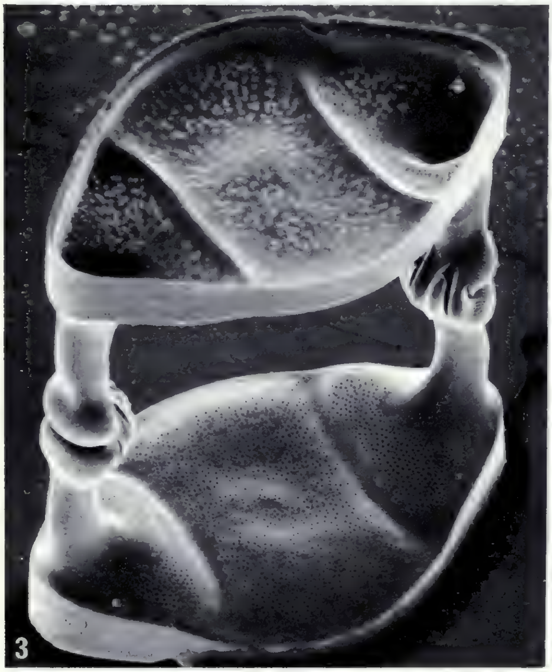
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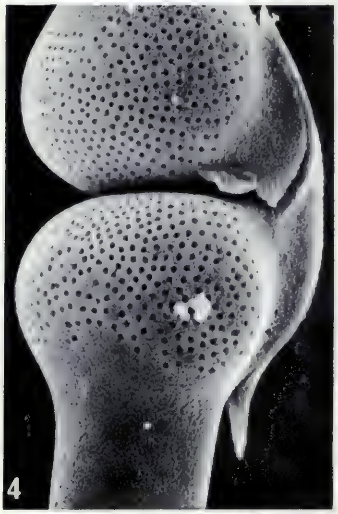
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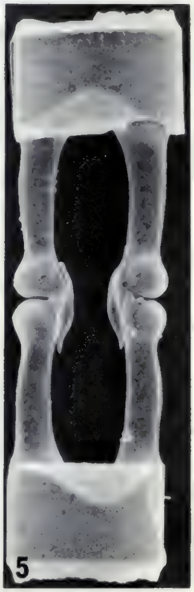
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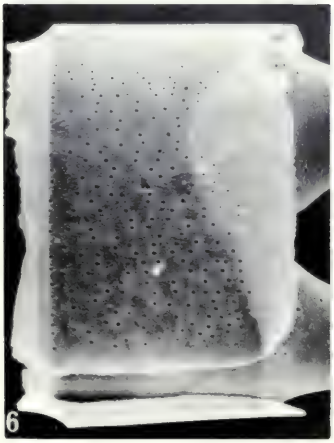
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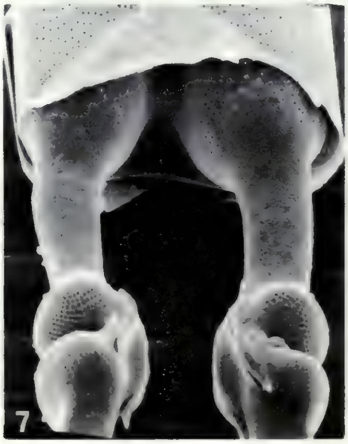
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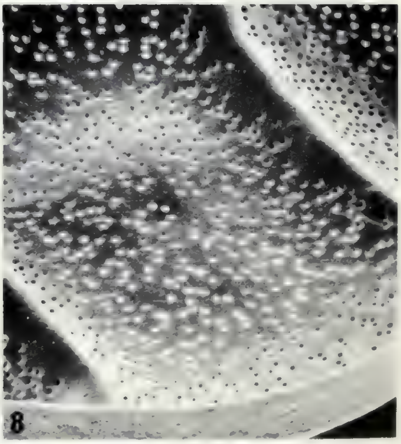
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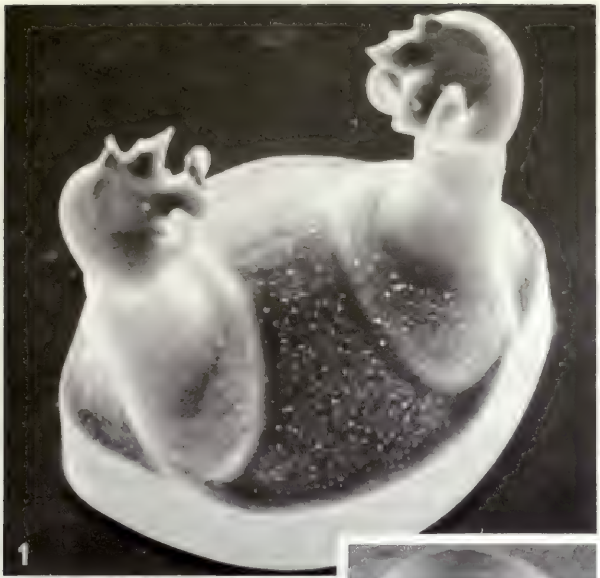
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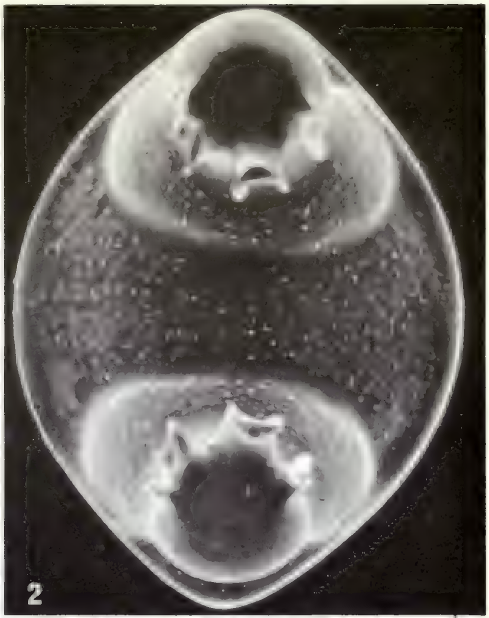
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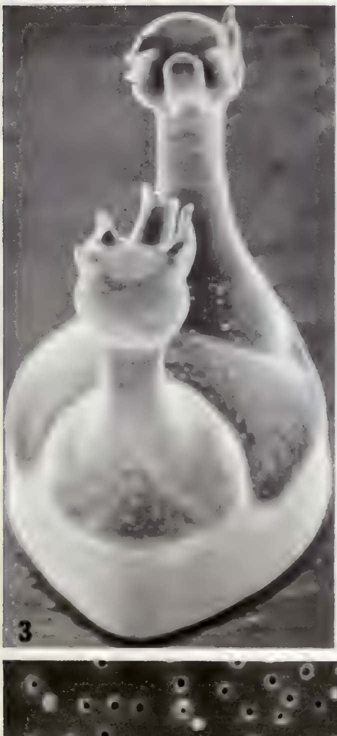
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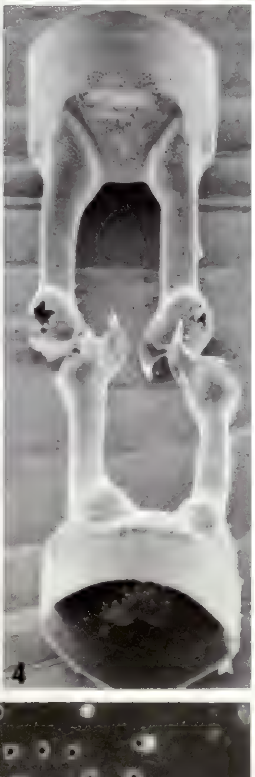
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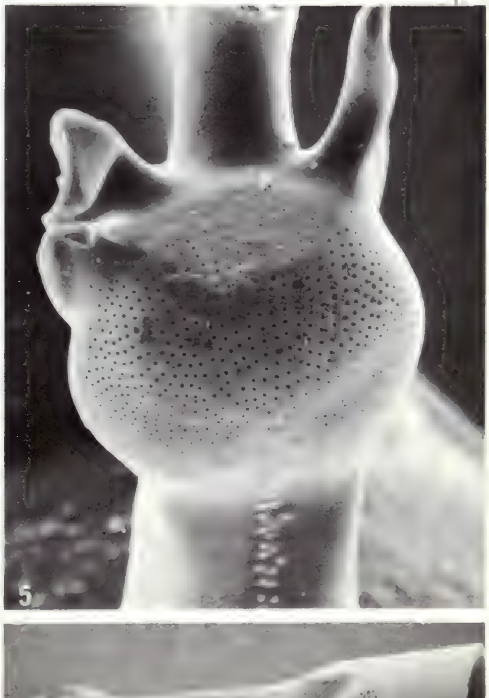
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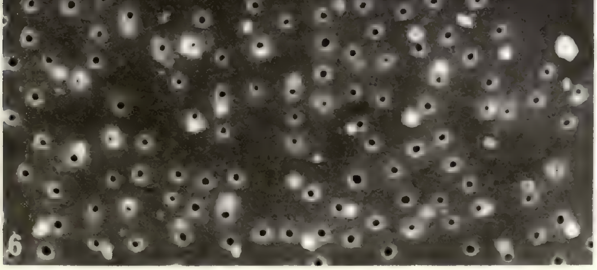
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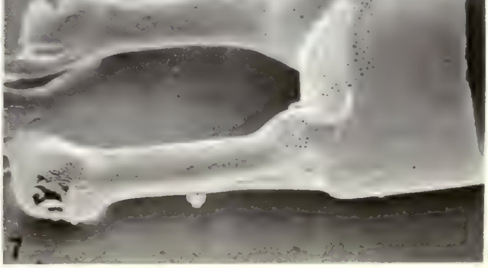
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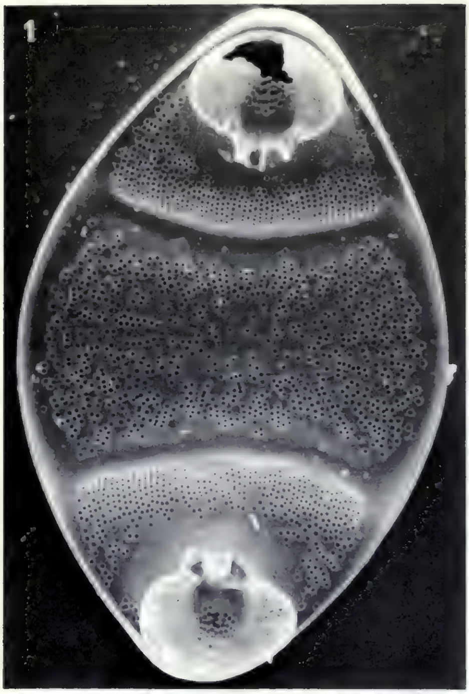
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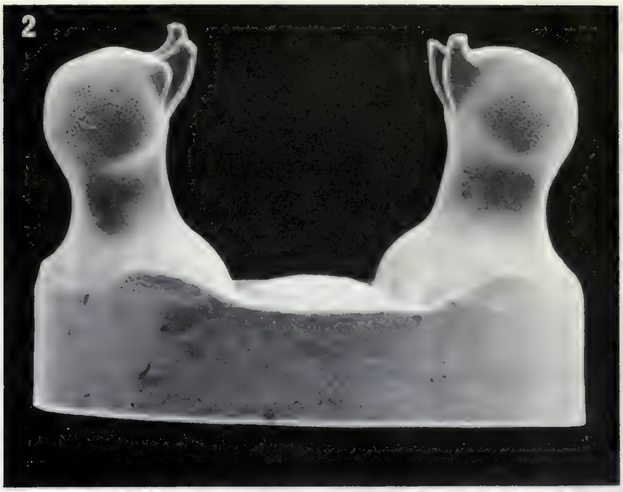
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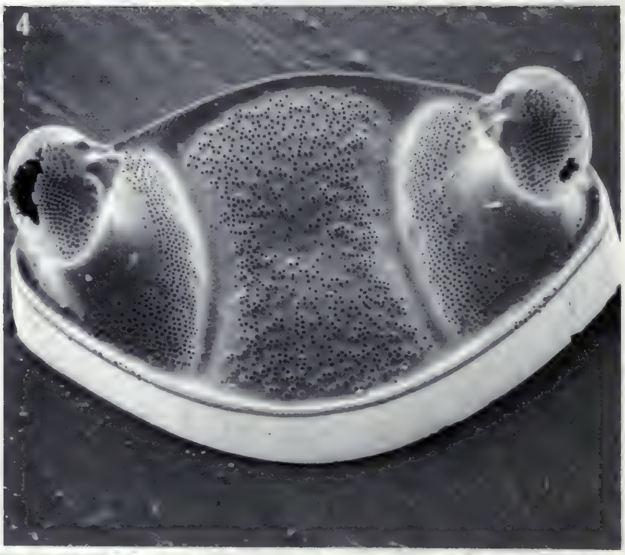
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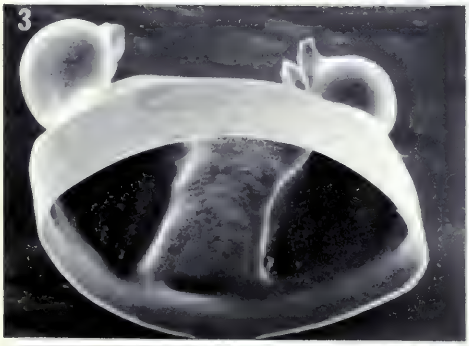
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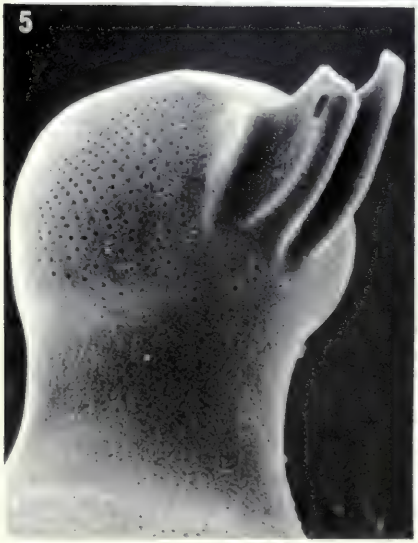
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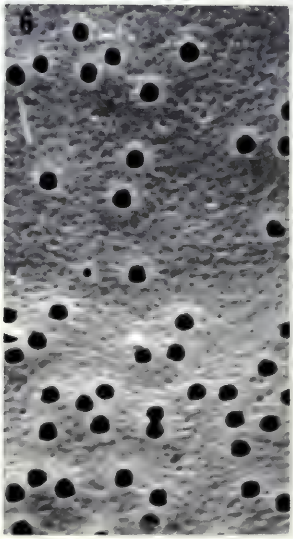
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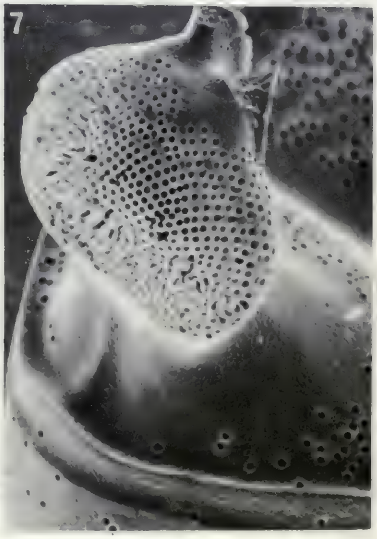
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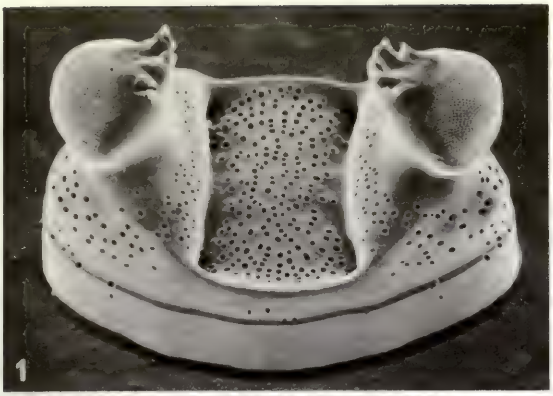
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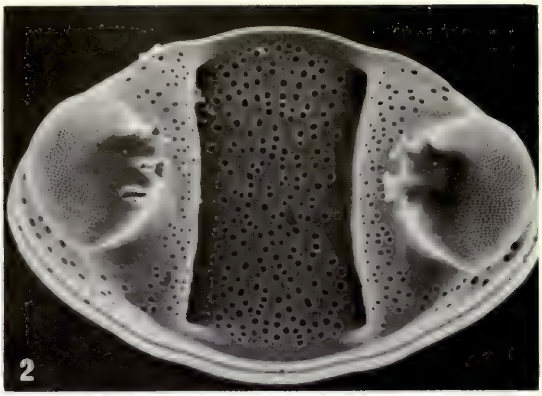
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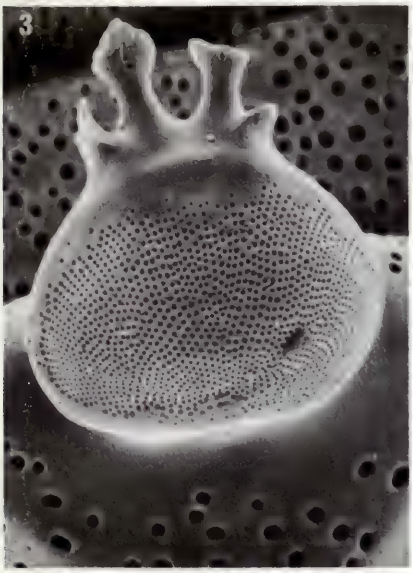
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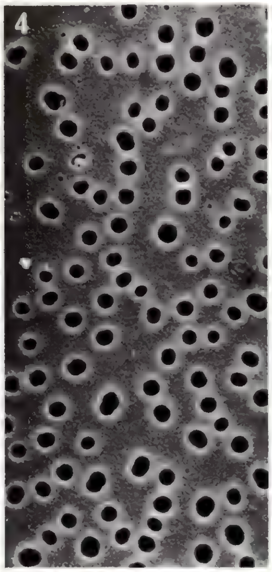
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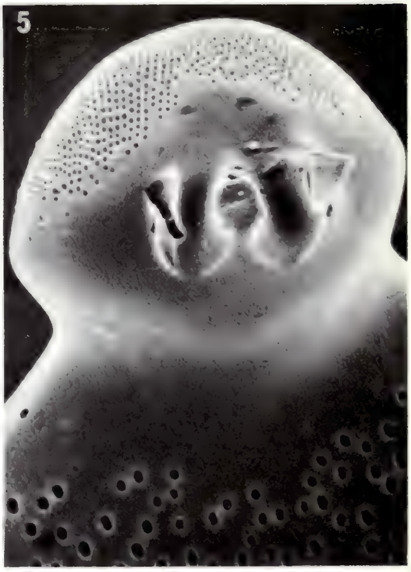
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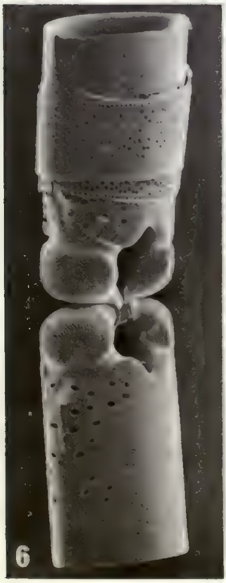
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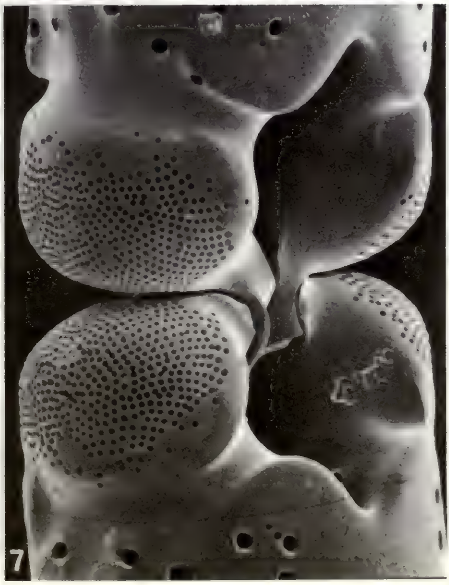
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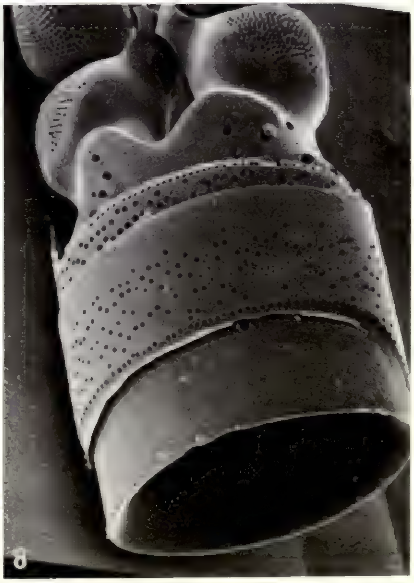
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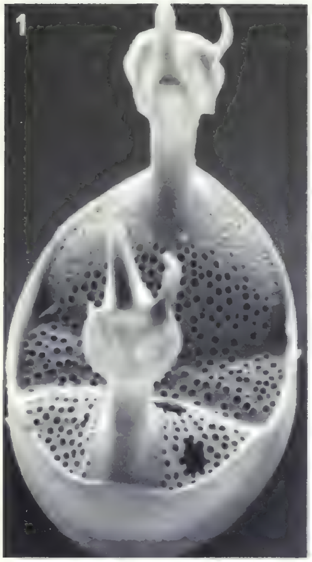
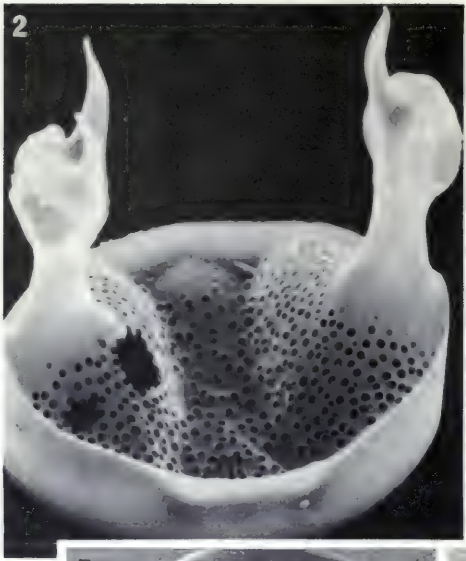
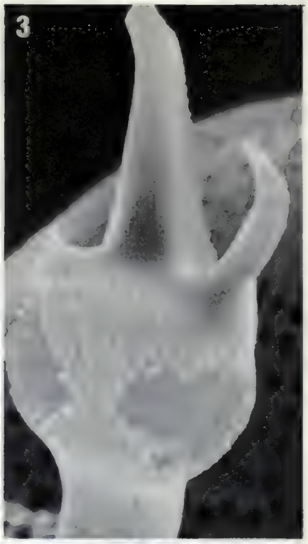
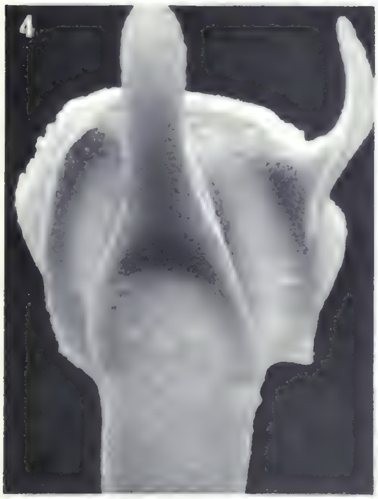
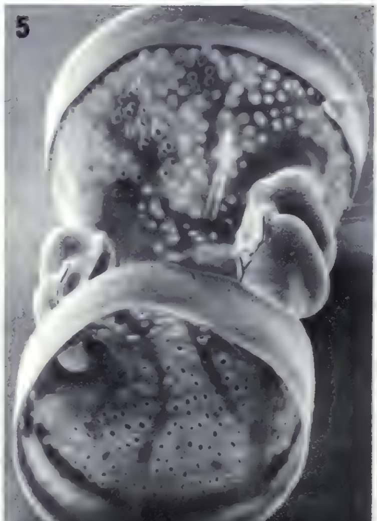
PLATE 14

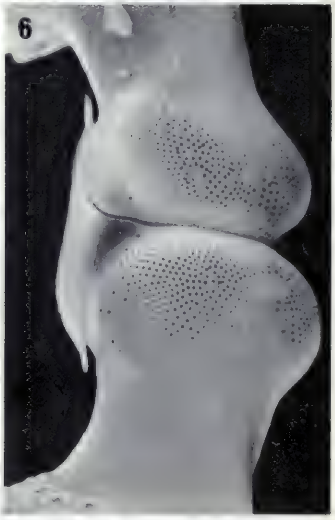


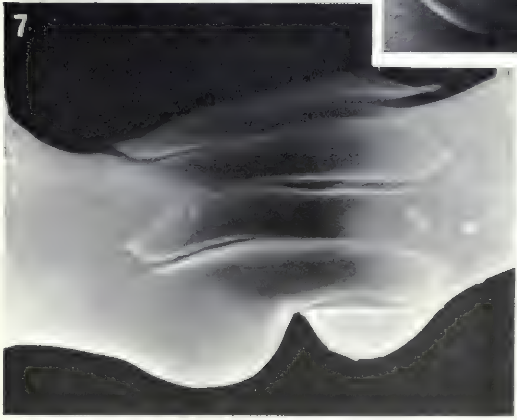


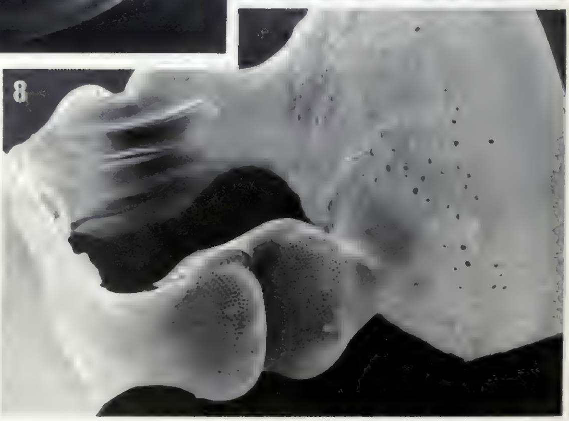


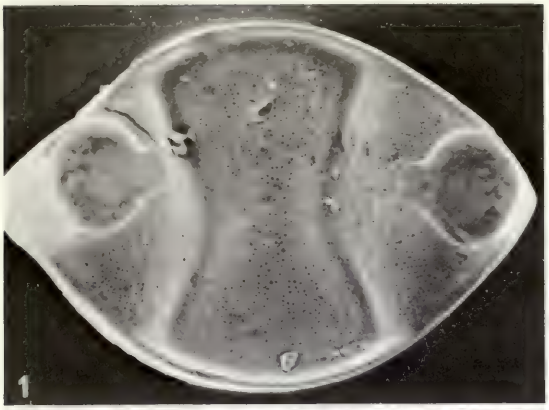








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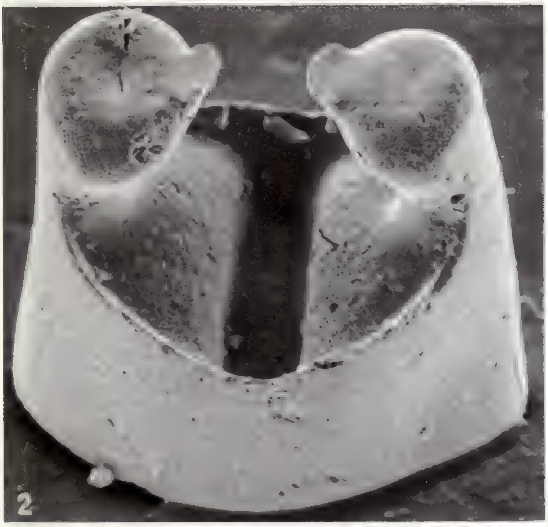
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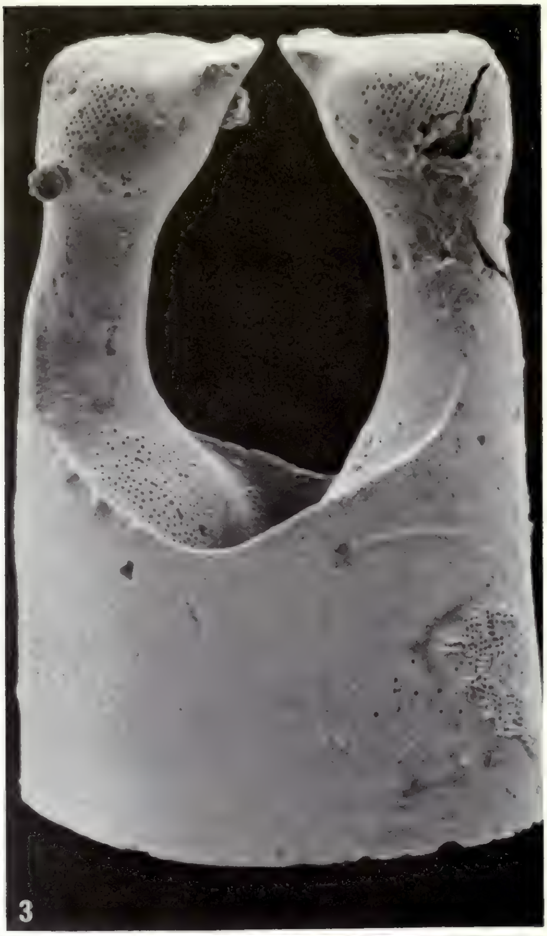
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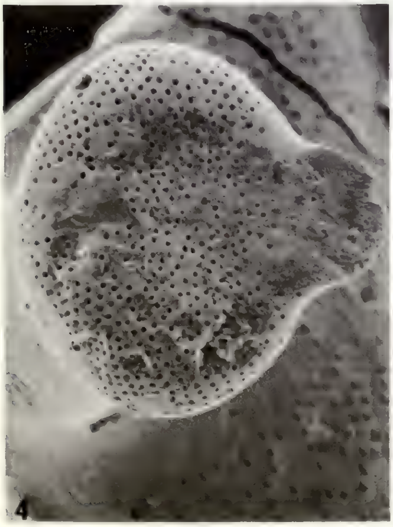
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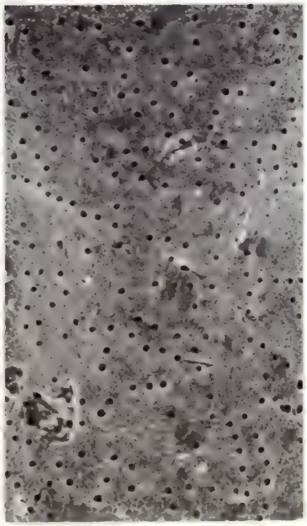

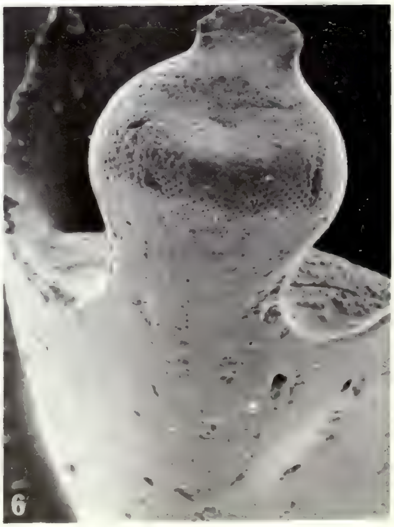
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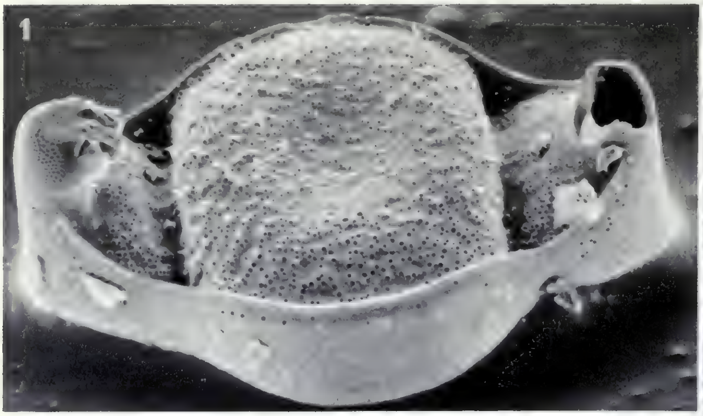
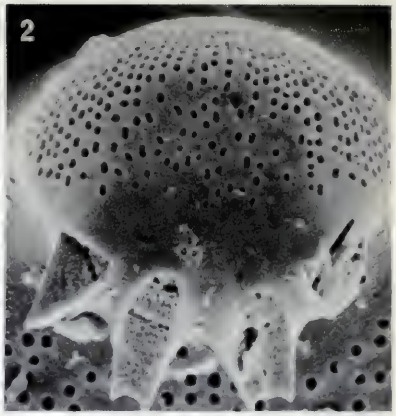
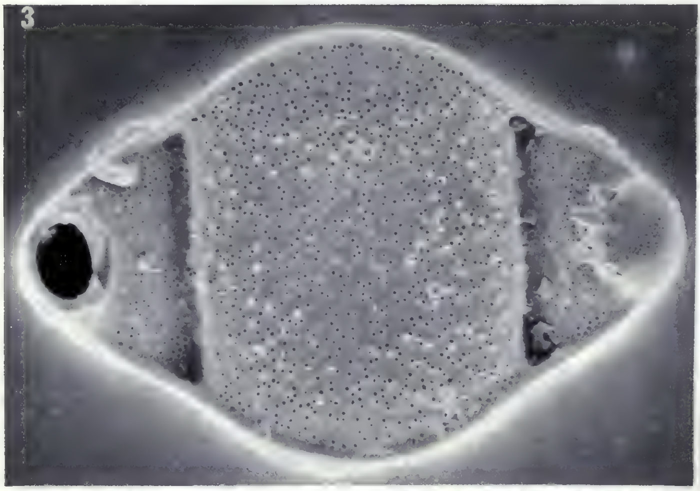
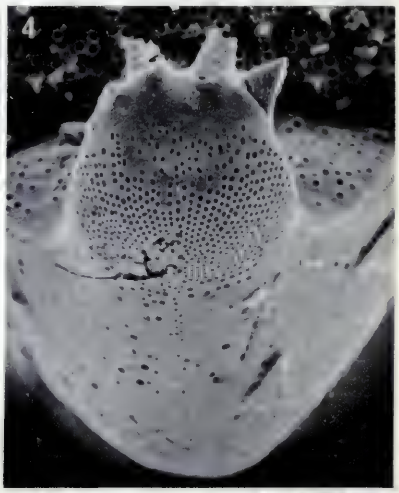
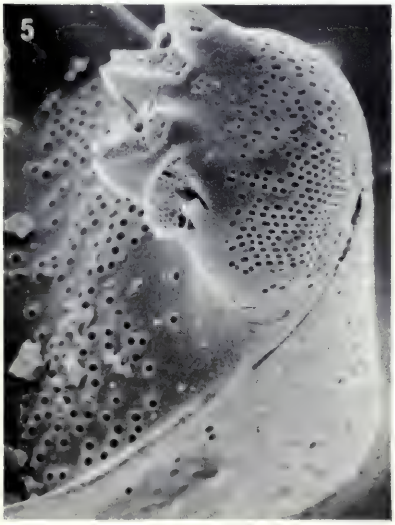
PLATE 16

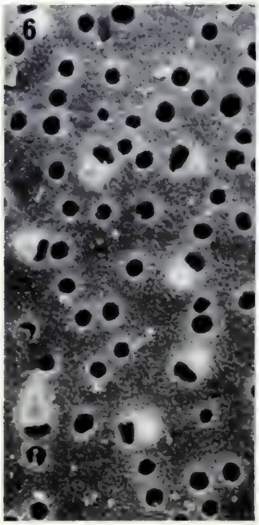












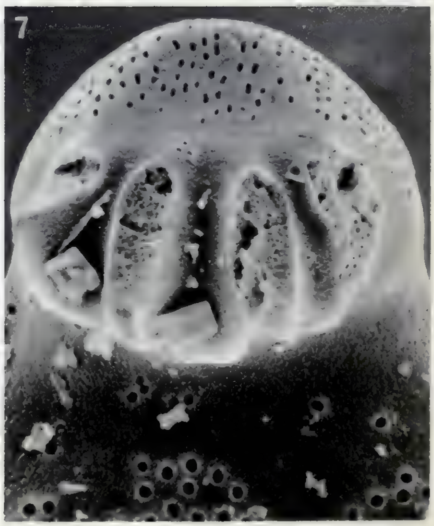
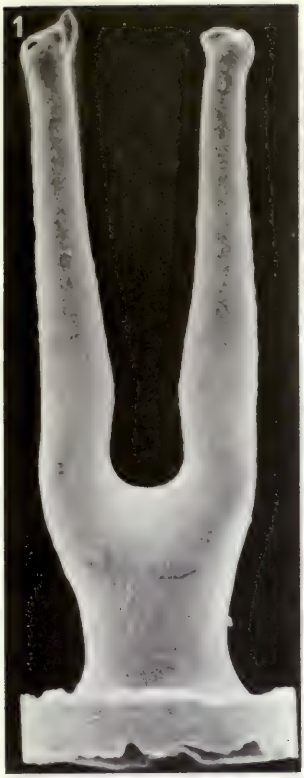


PLATE 17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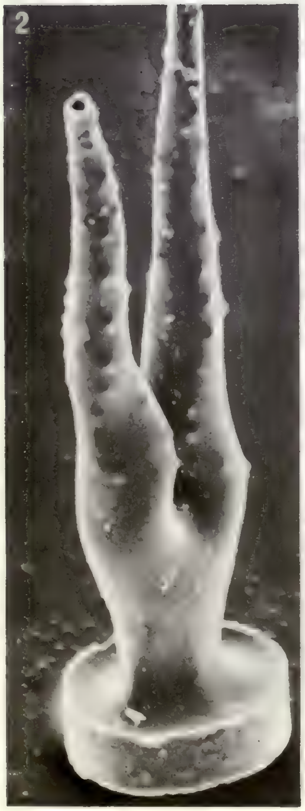
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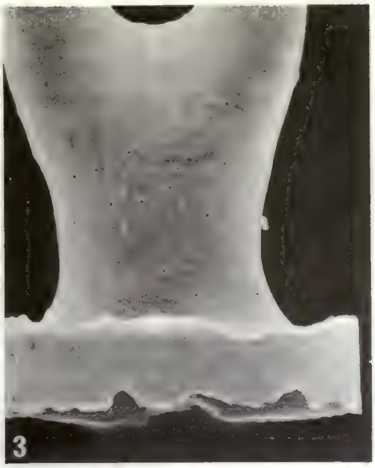
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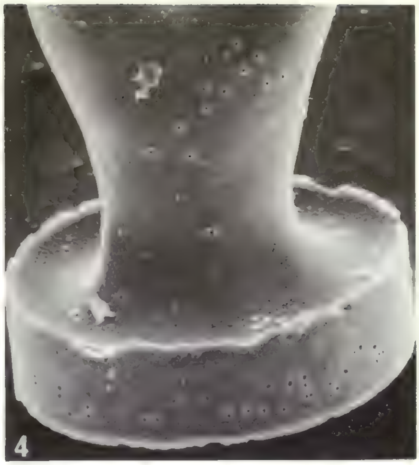
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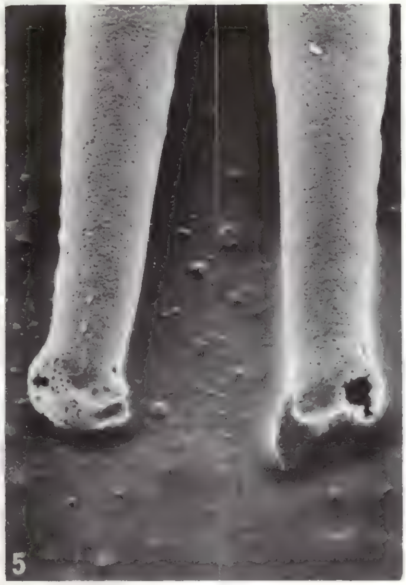
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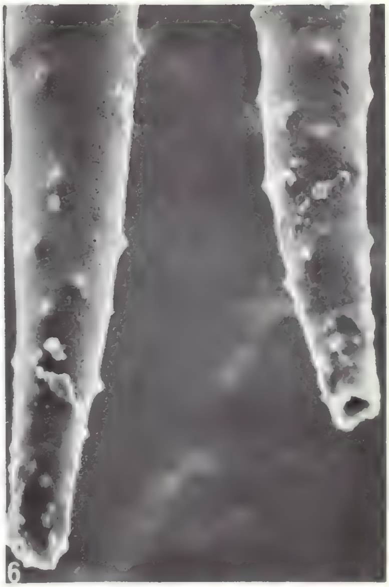
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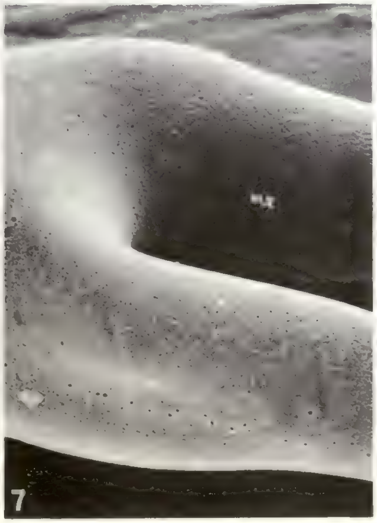
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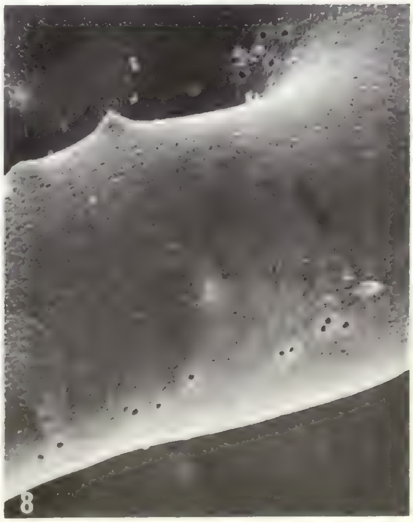
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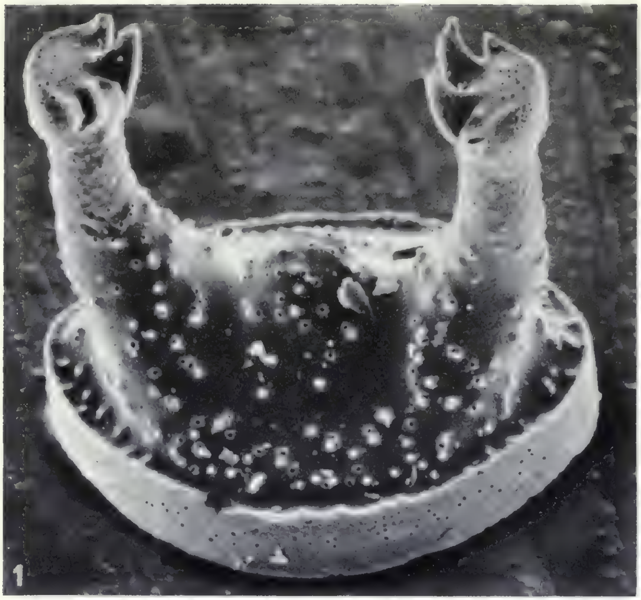
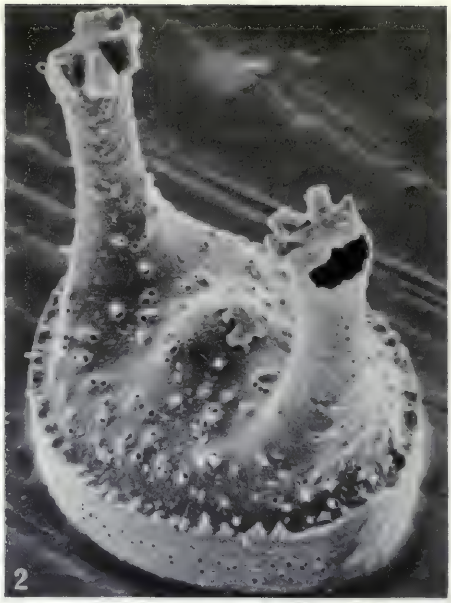
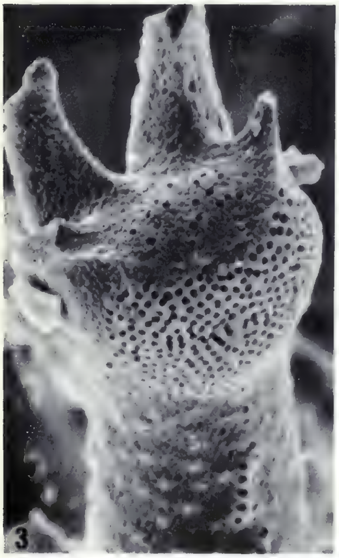
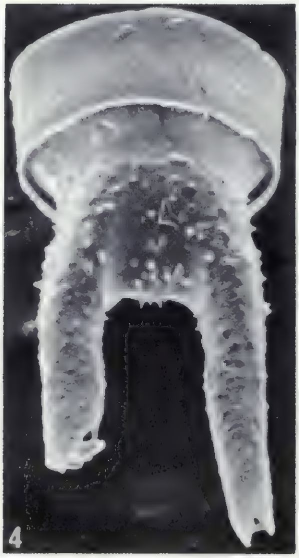
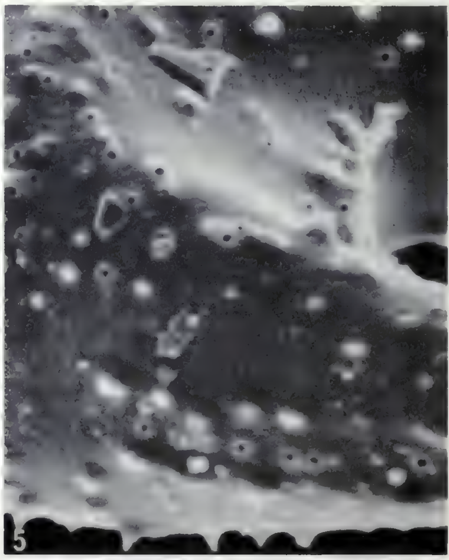
PLATE 18

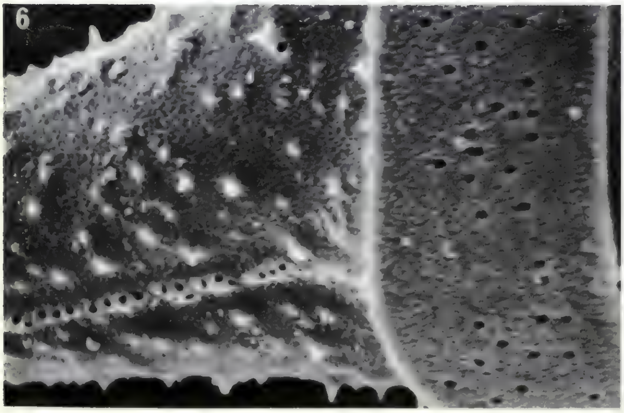


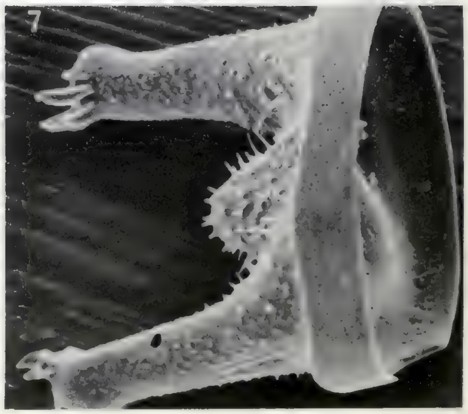


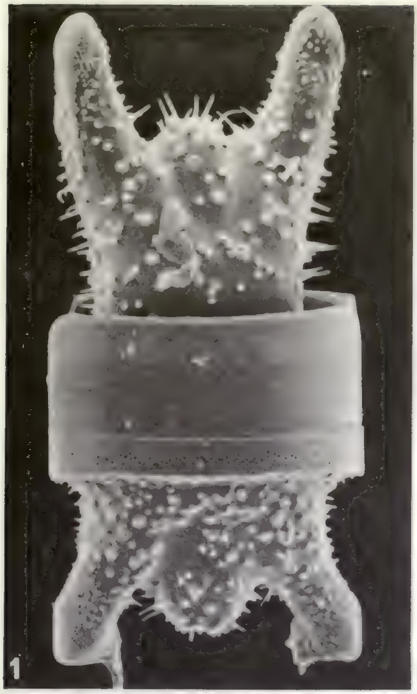








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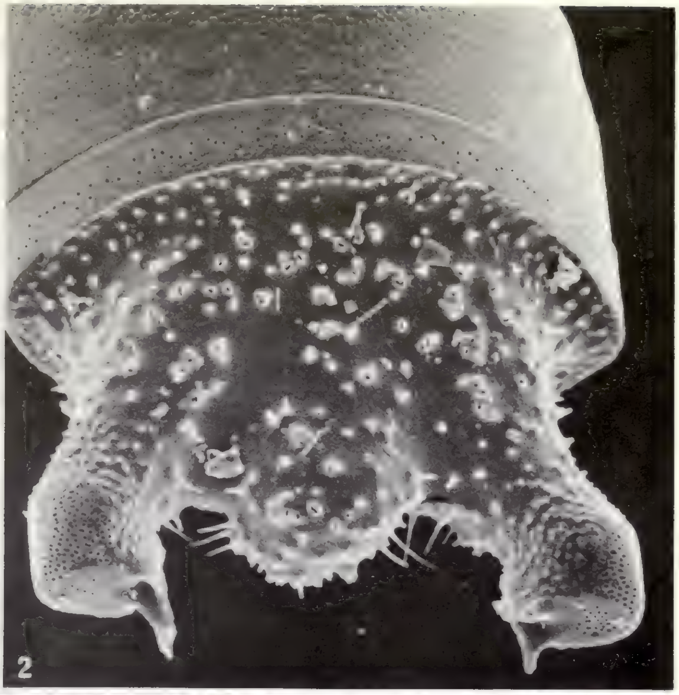
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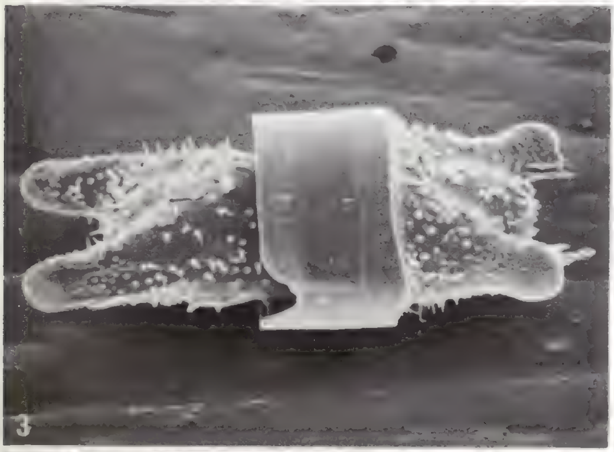
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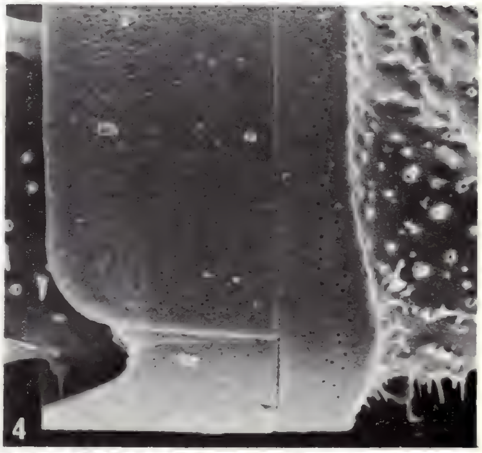
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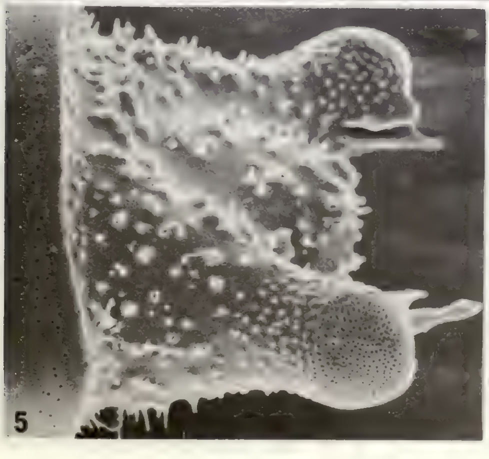
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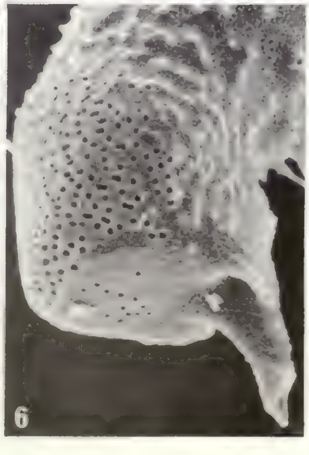
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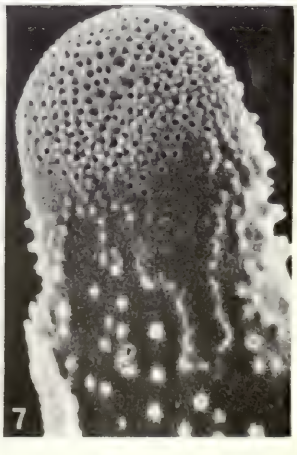
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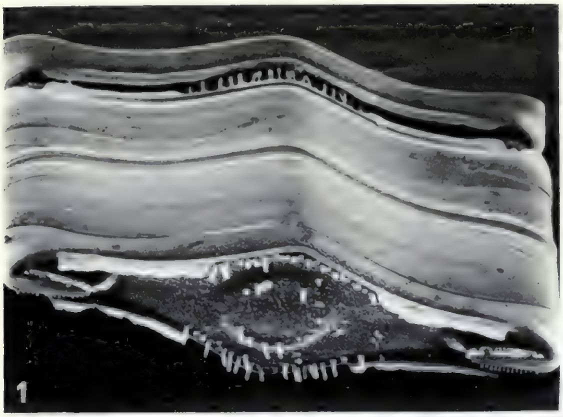
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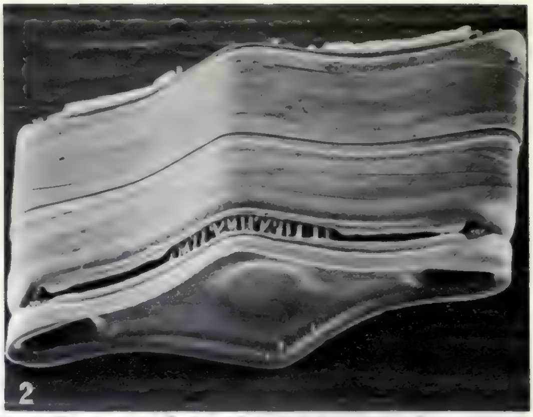
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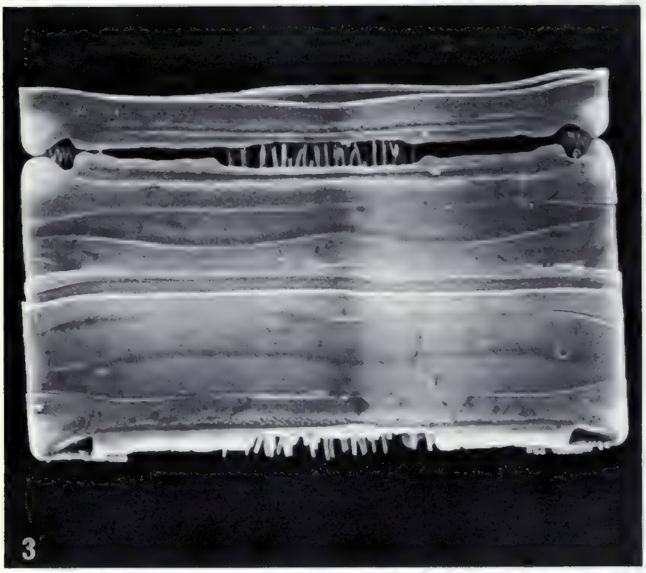
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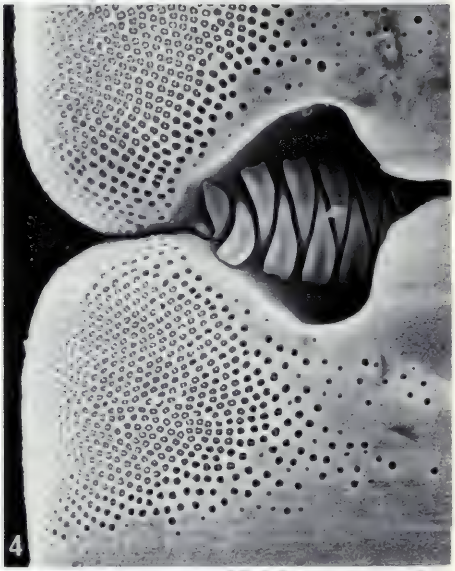
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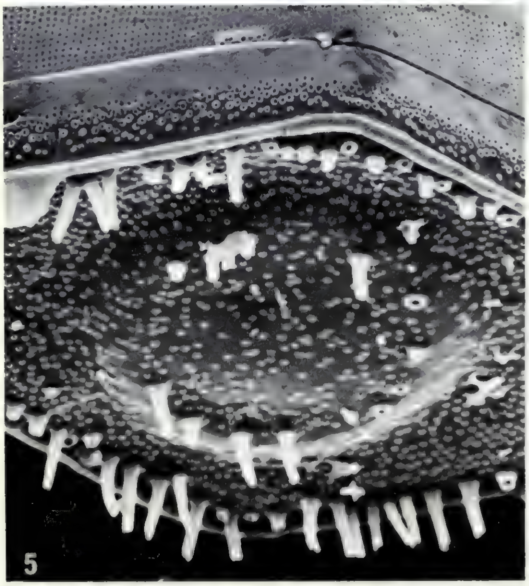
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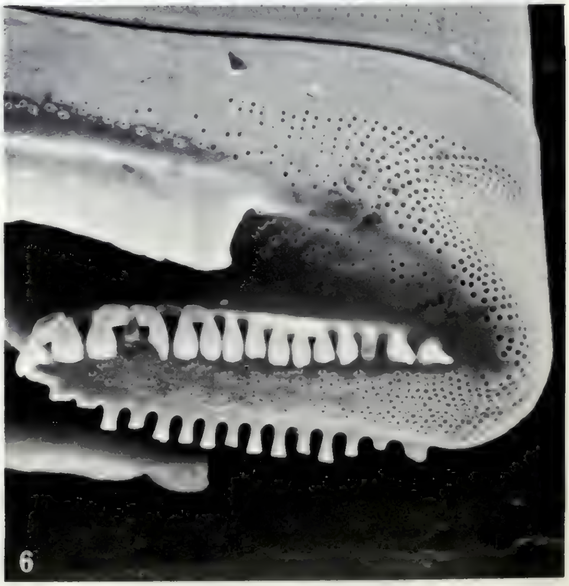
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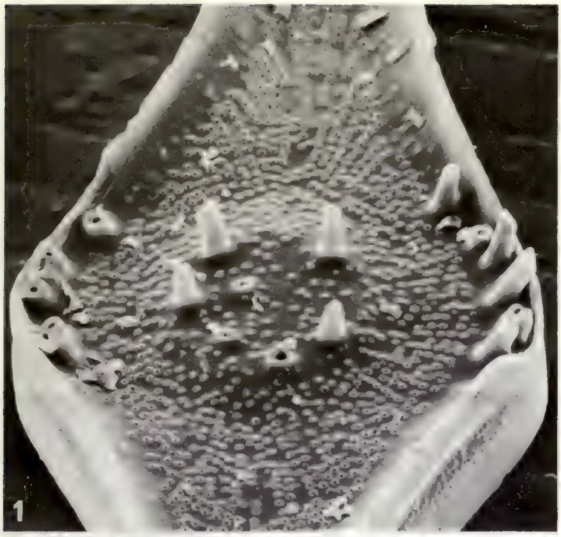
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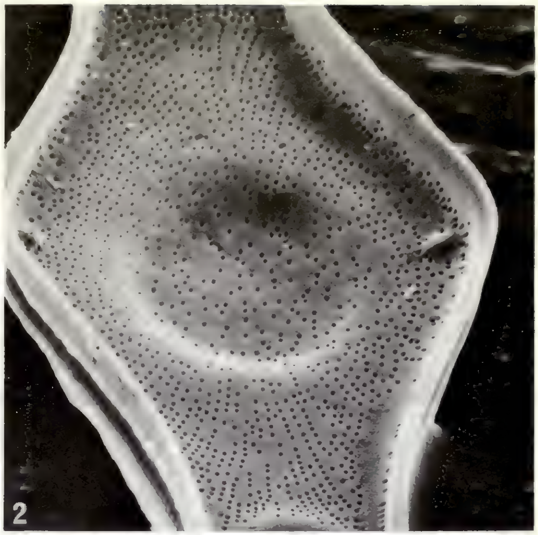
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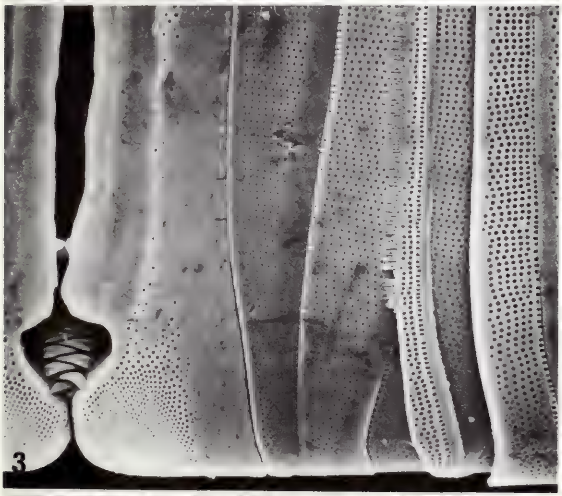
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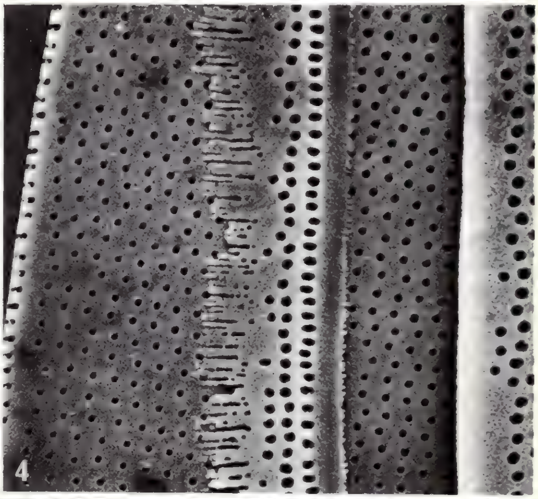
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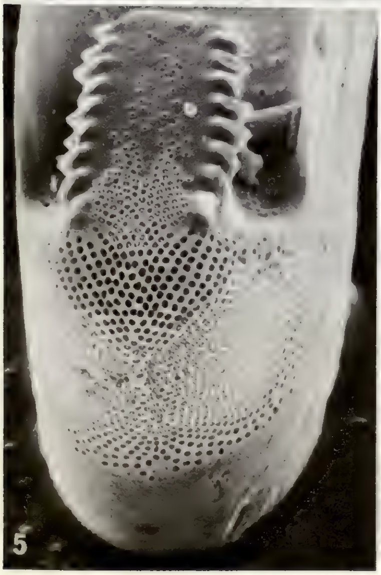
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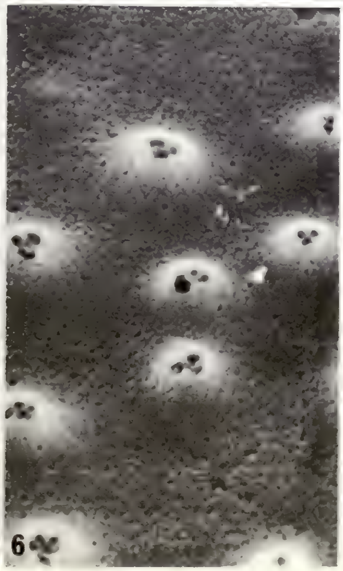
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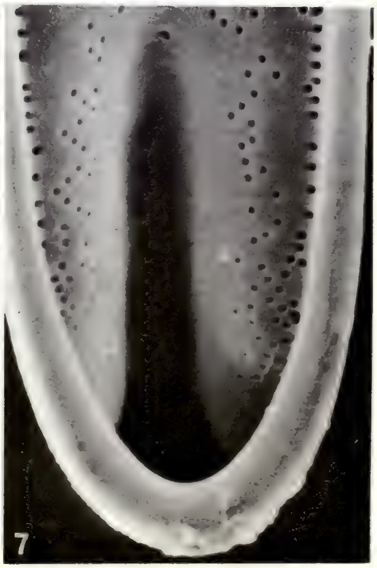
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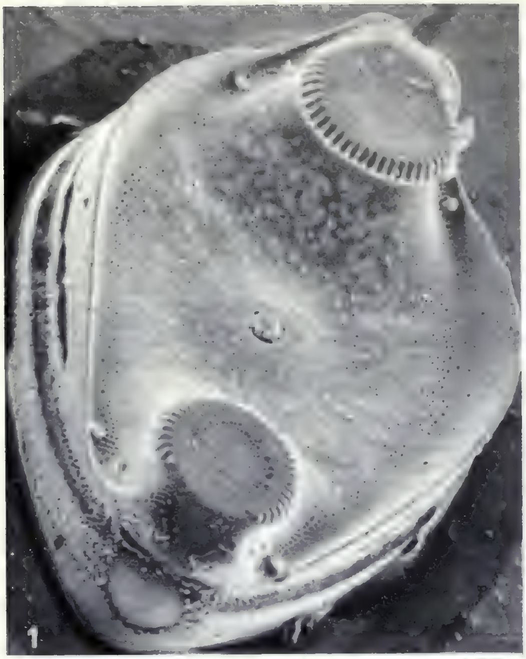
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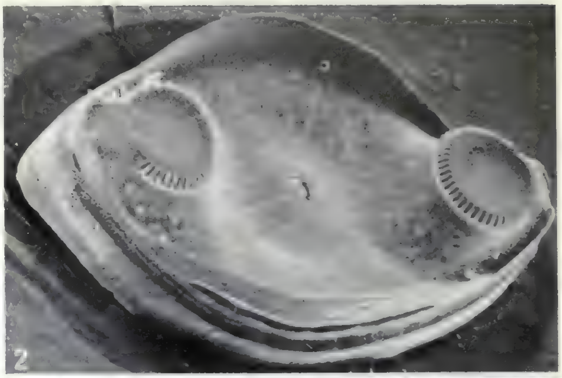
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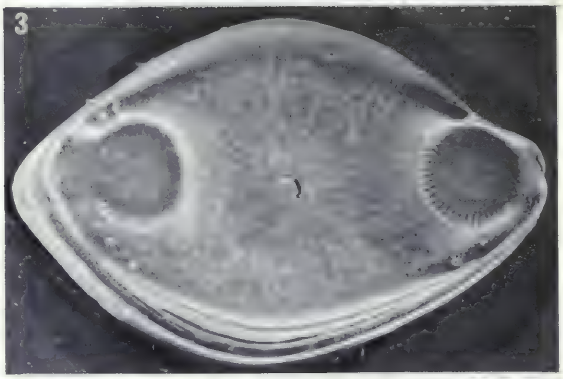
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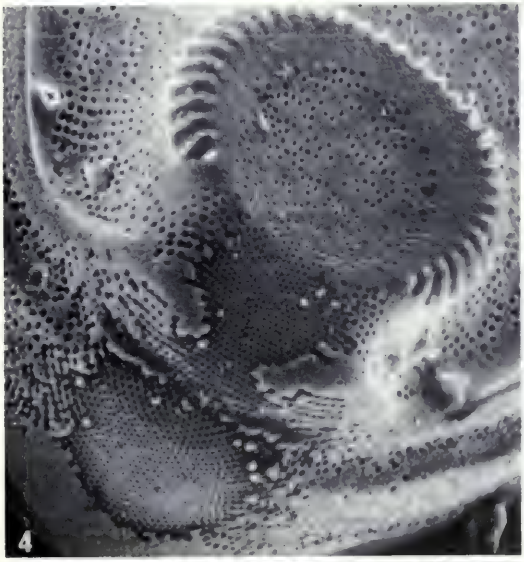
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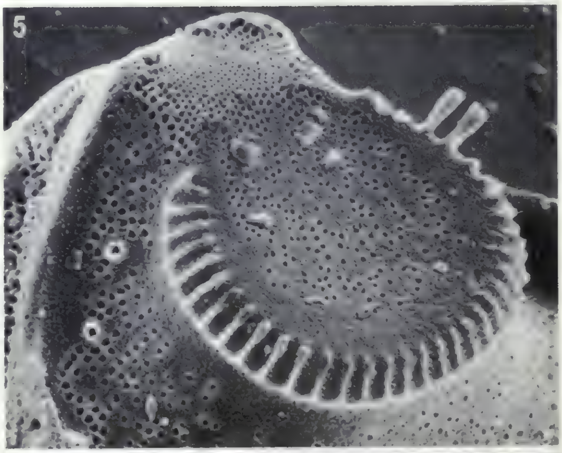
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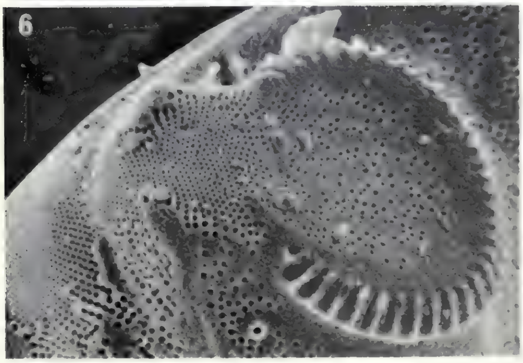
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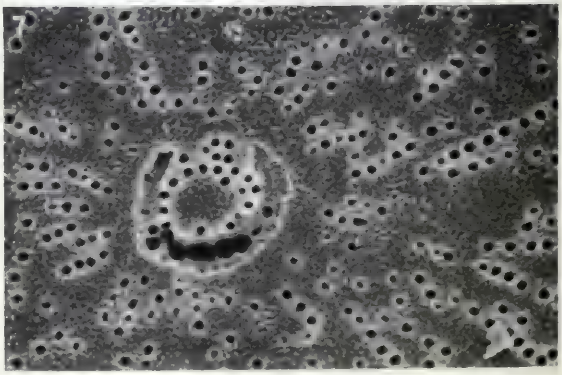
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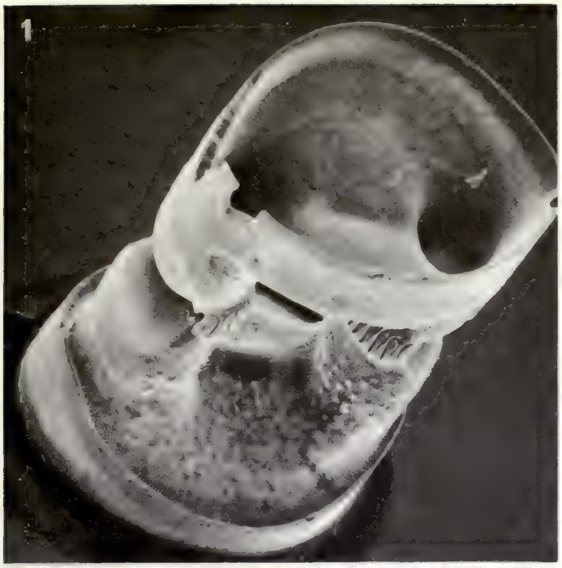
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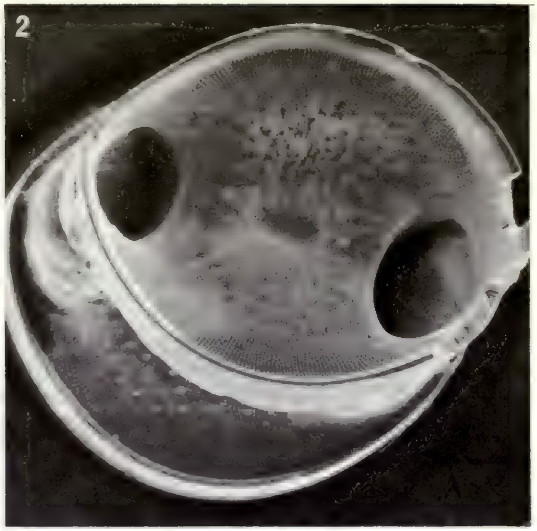
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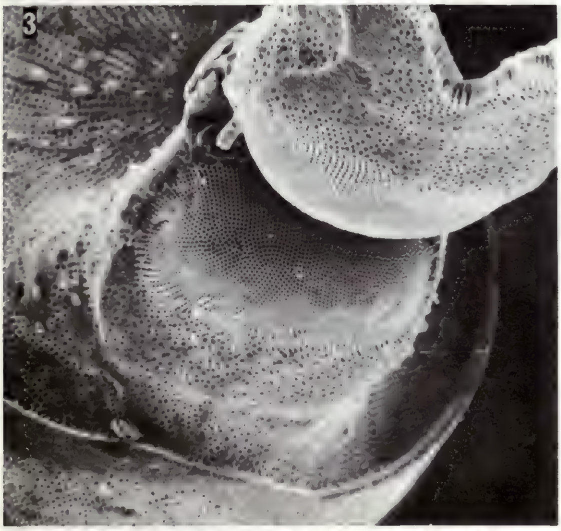
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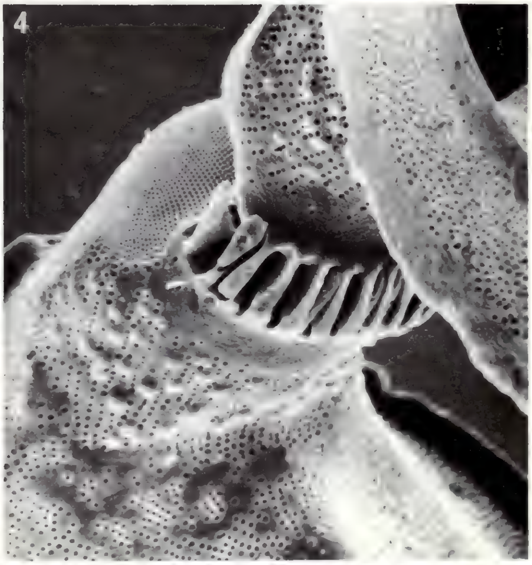
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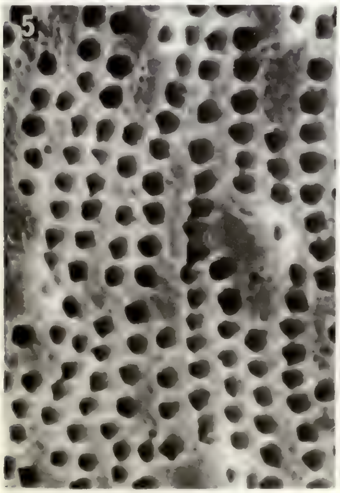
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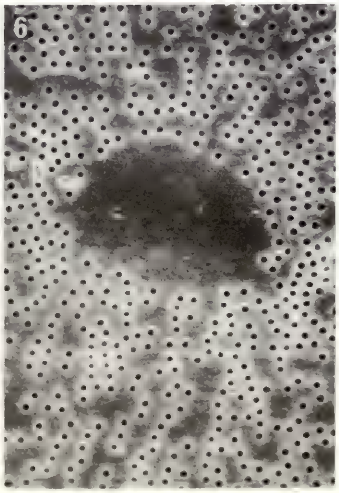
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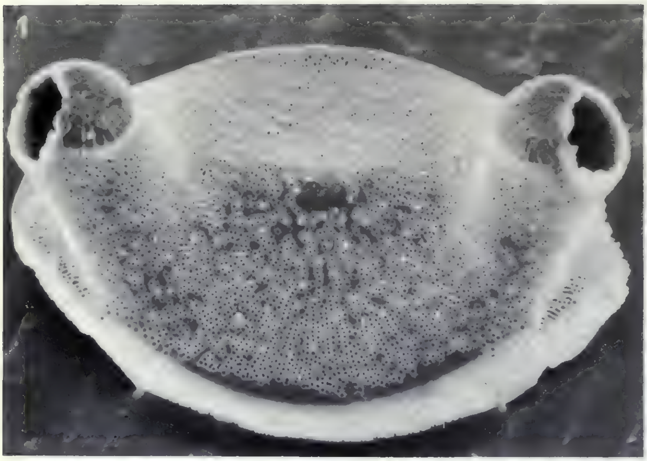
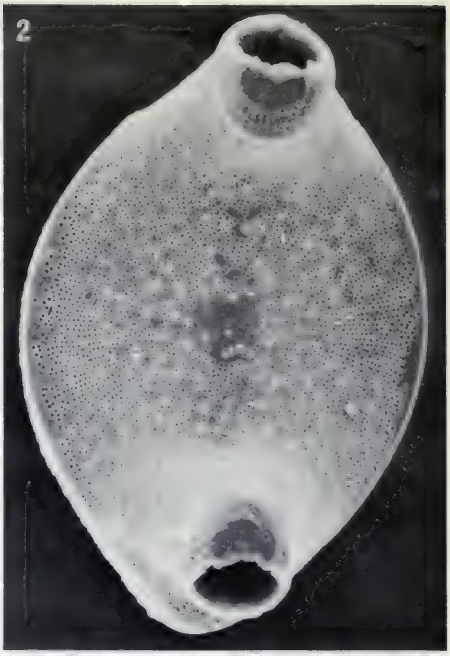
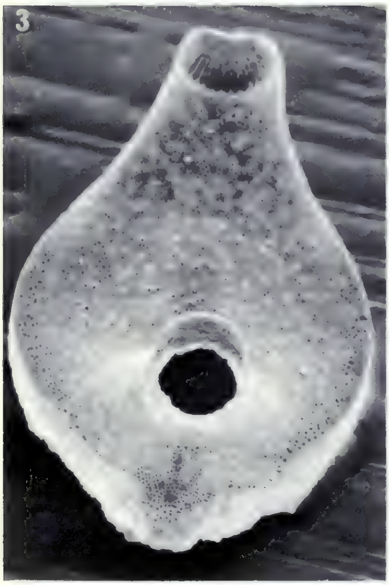
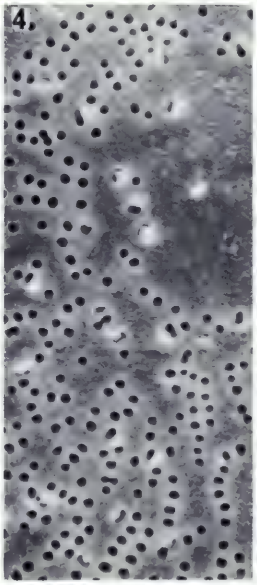
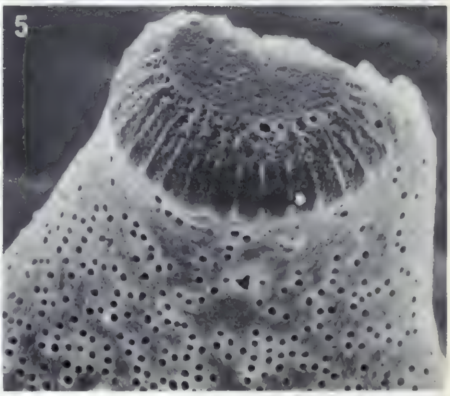
PLATE 24

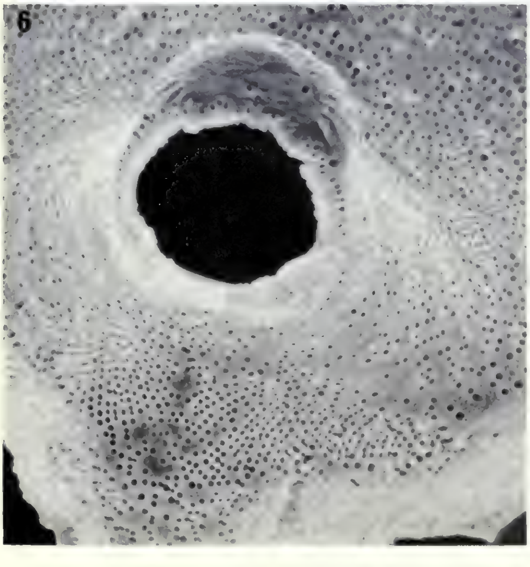


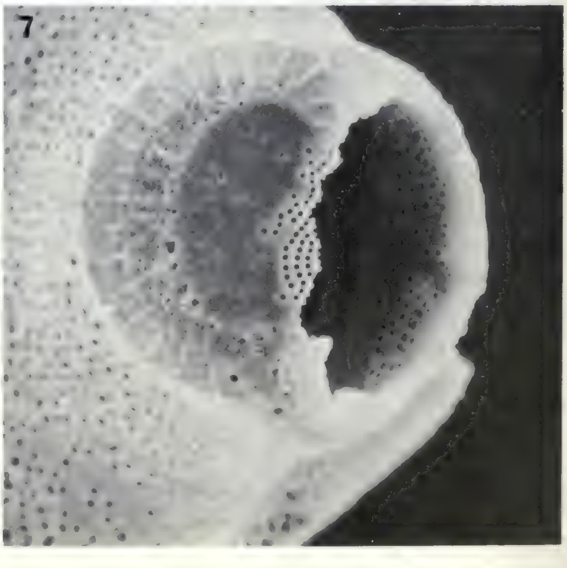


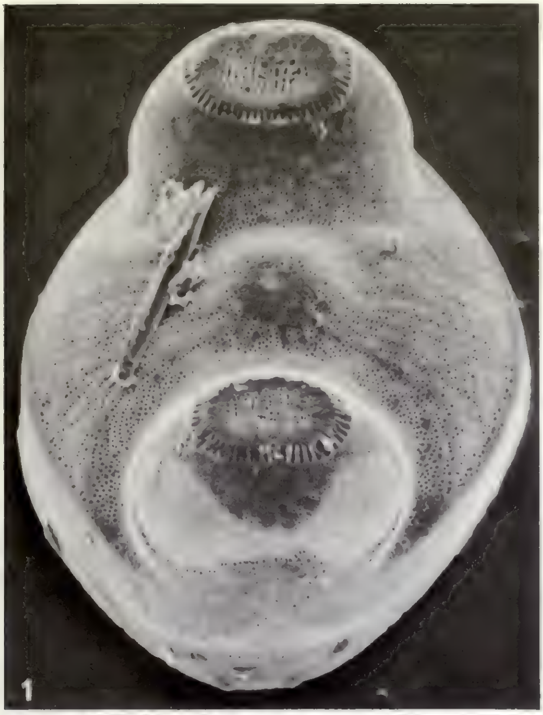








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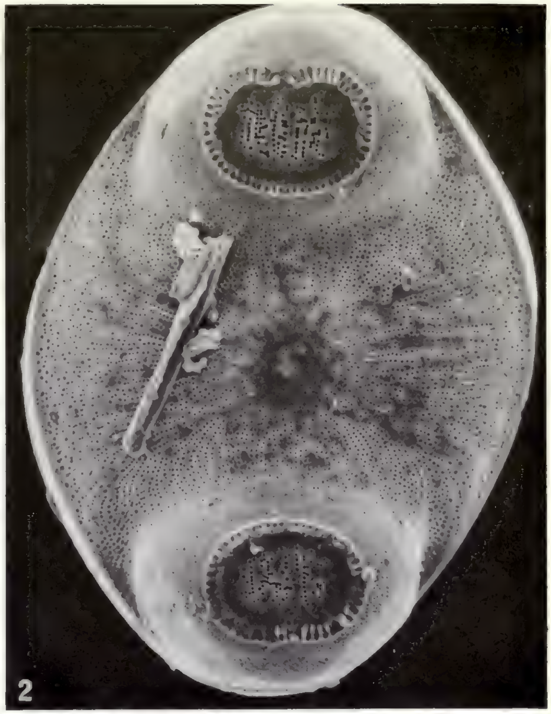
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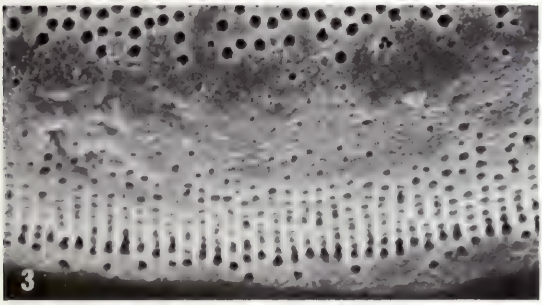
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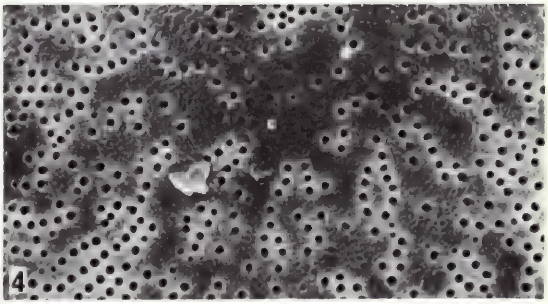
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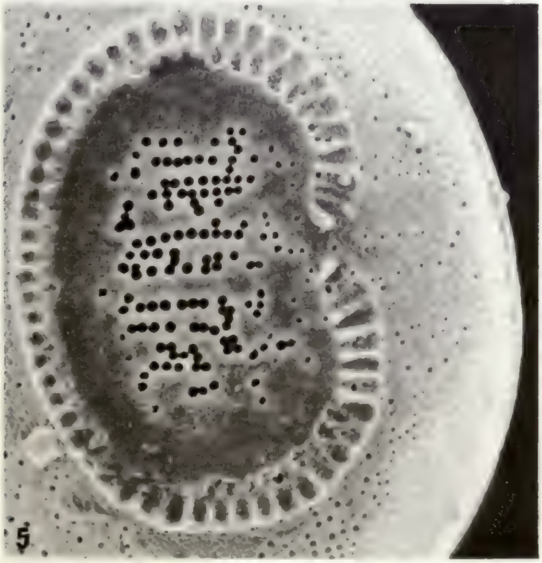
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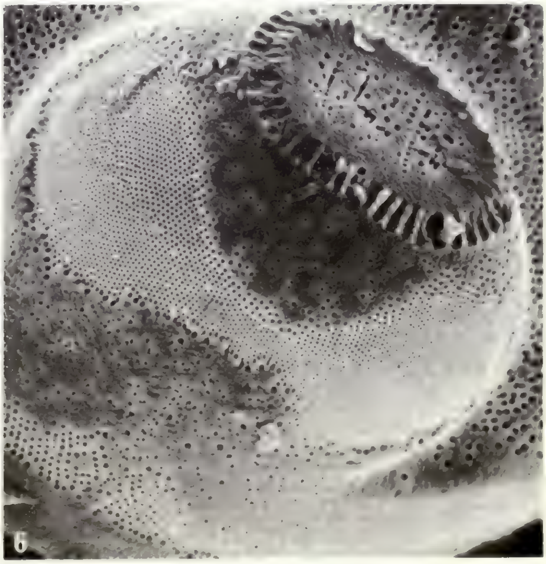
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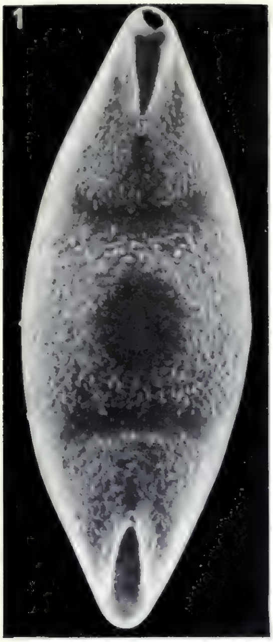
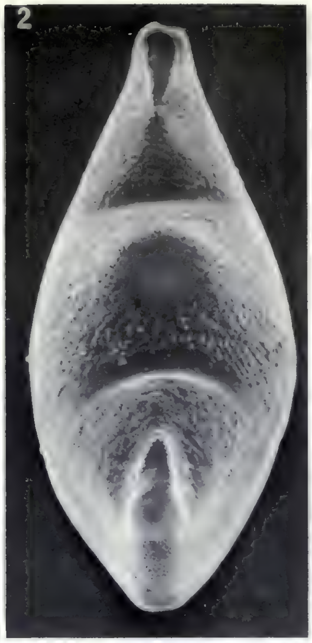
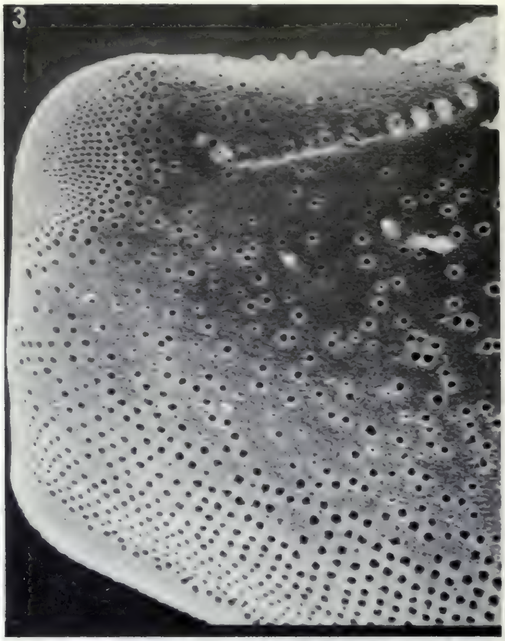
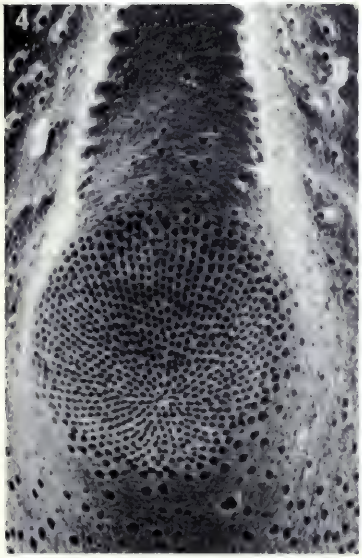
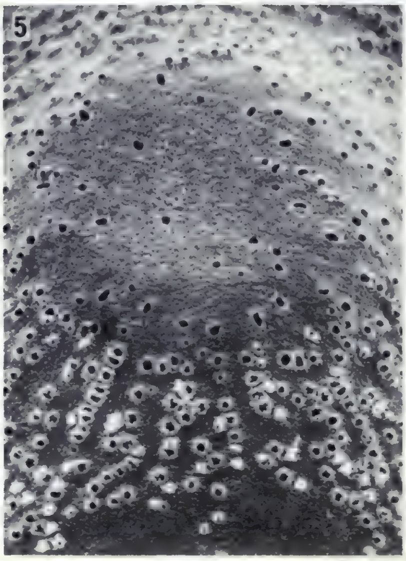
PLATE 26

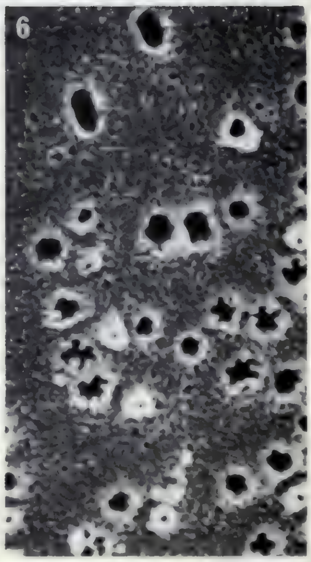


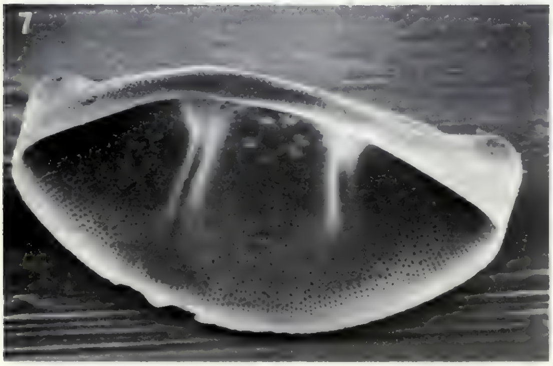












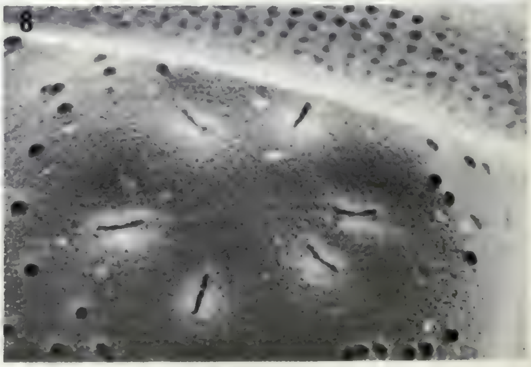
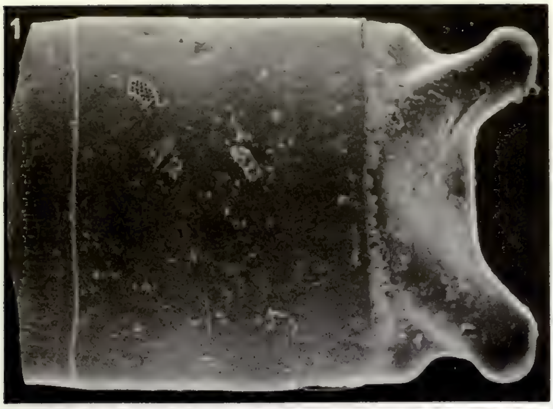
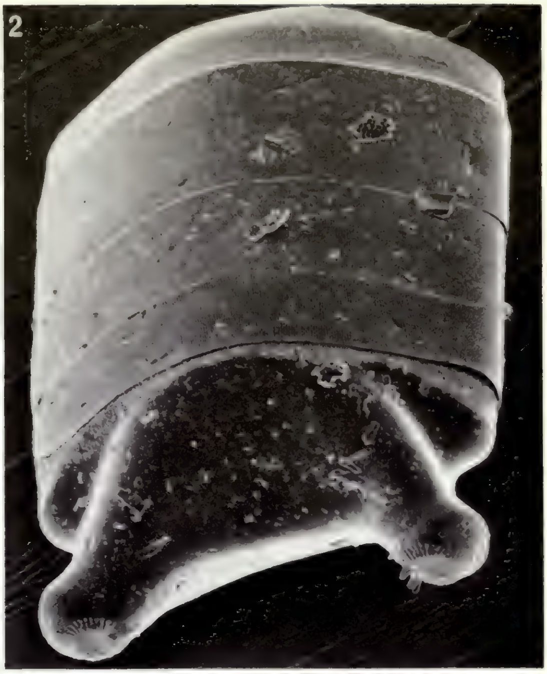
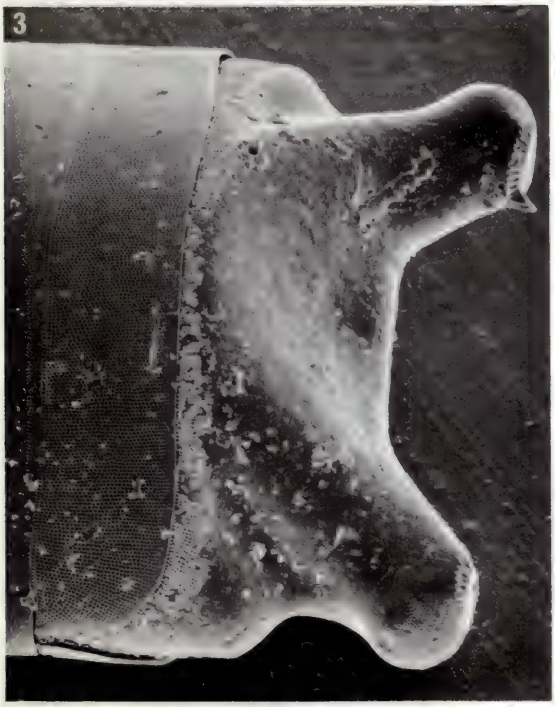
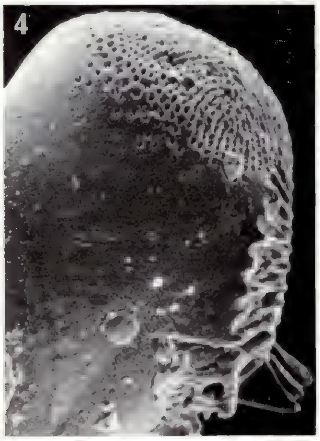


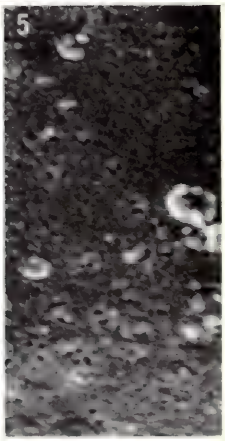
PLATE 27

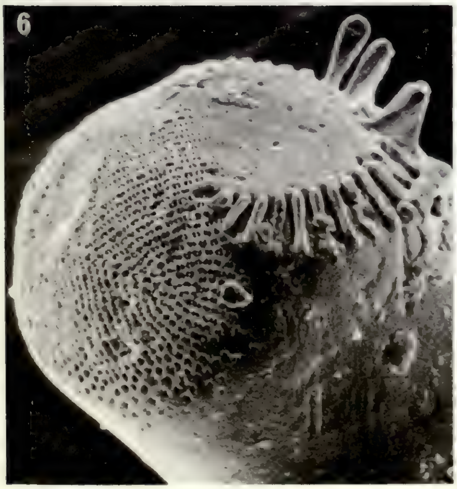


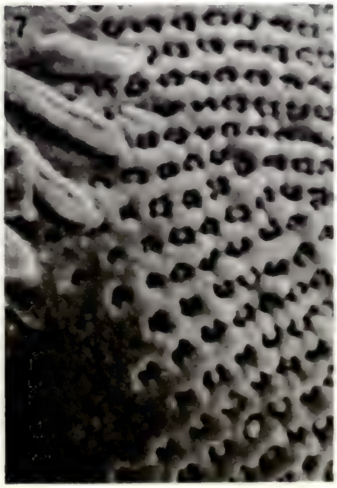


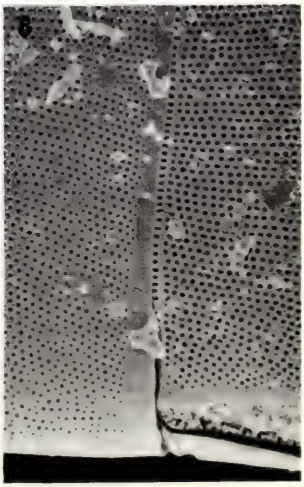


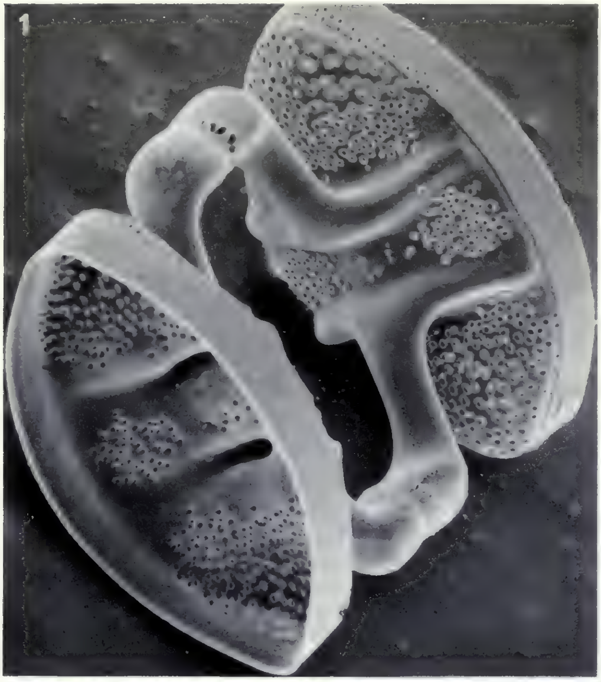








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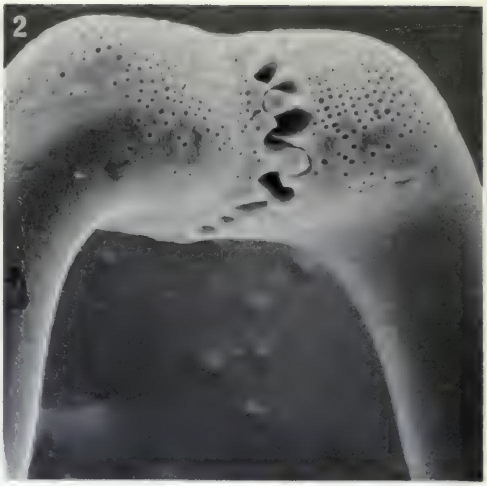
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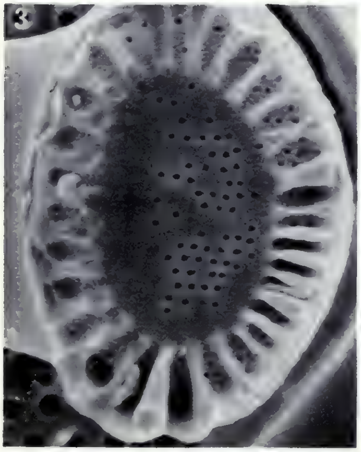
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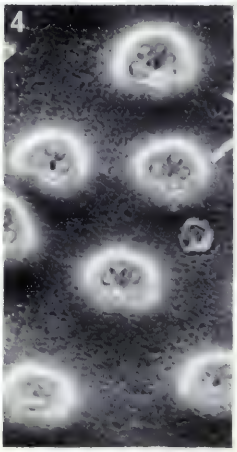
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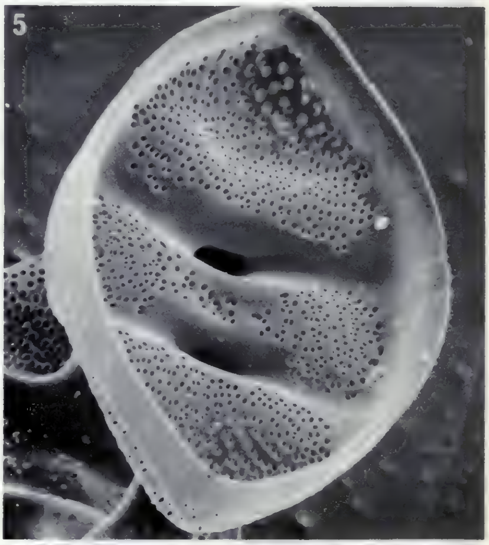
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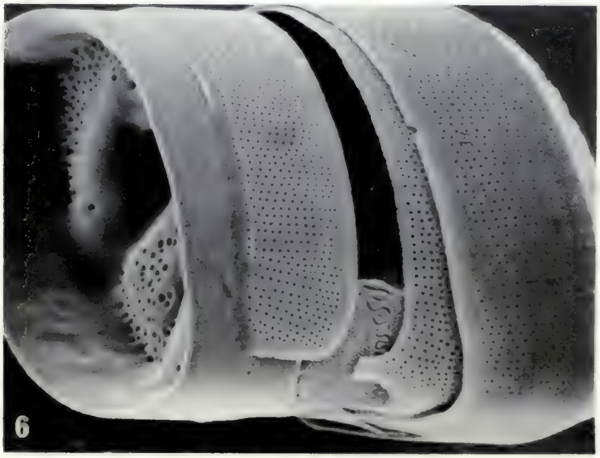
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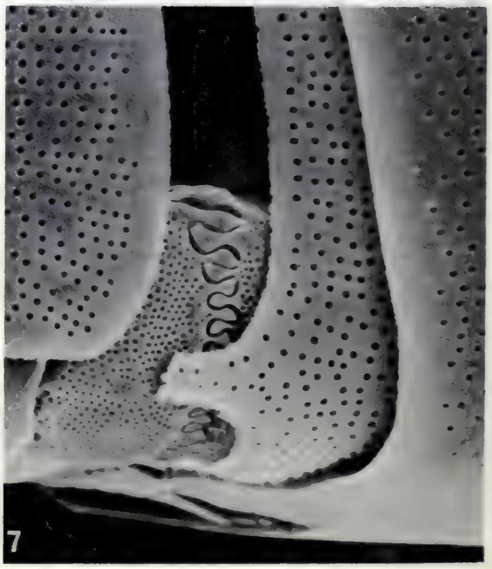
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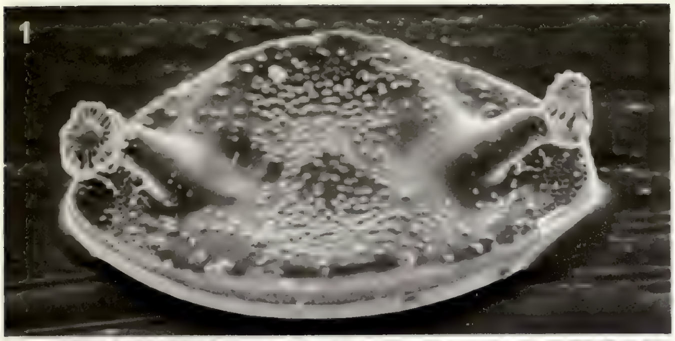
PLATE 29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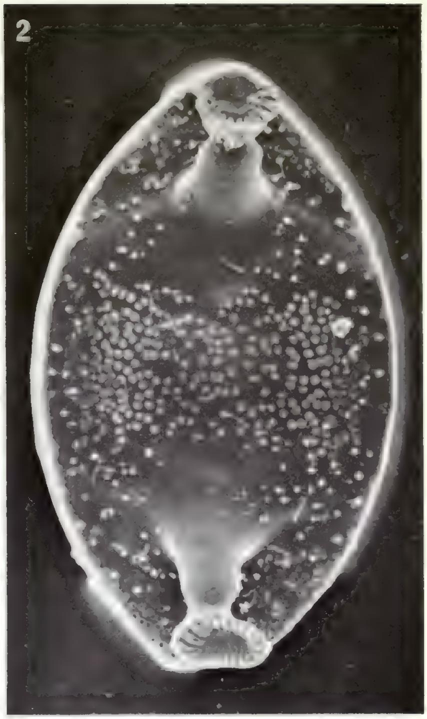
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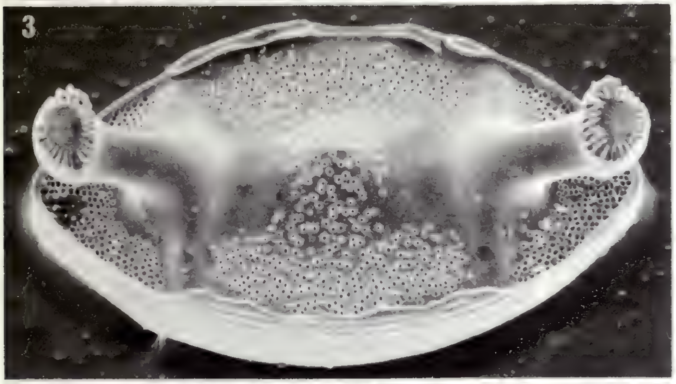
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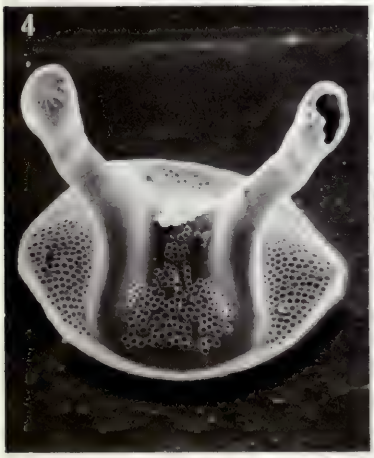
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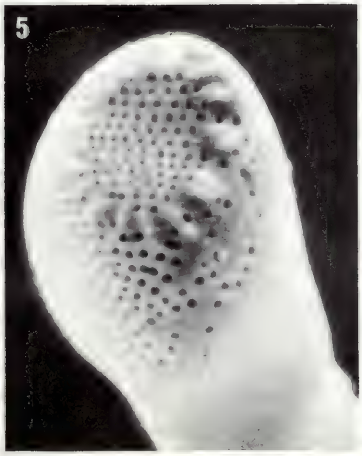
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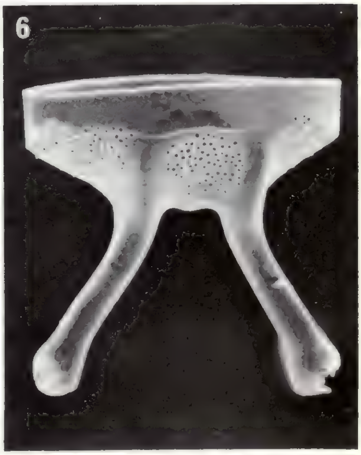
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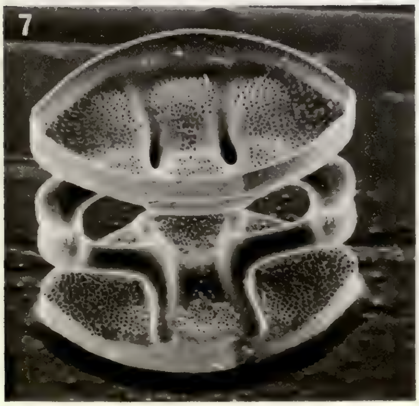
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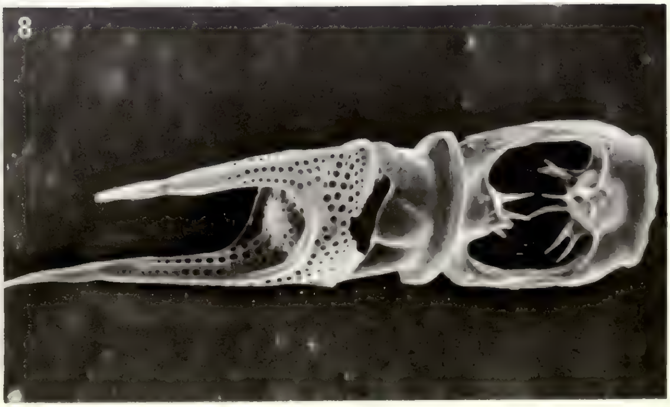
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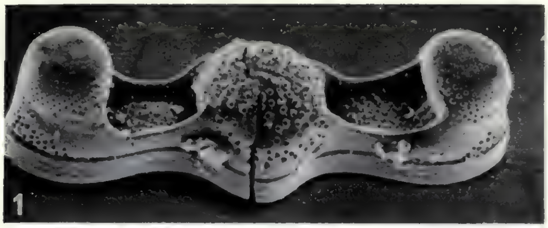
PLATE 30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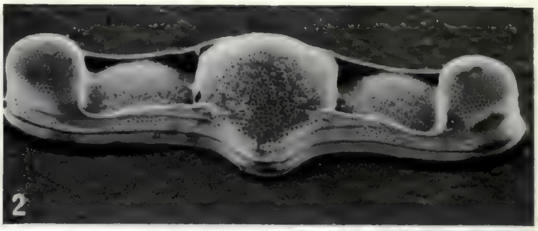
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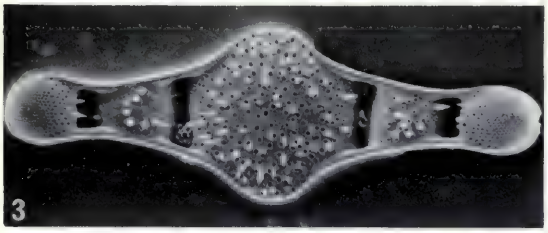
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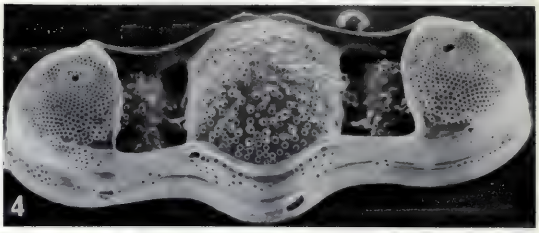
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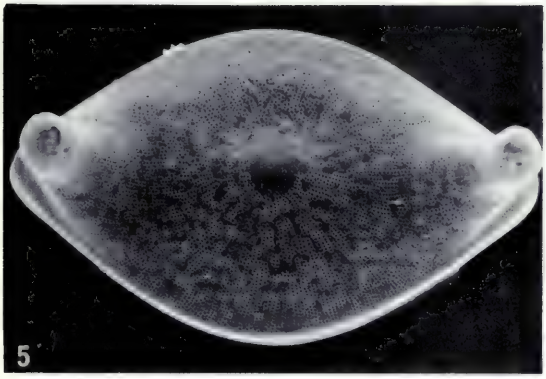
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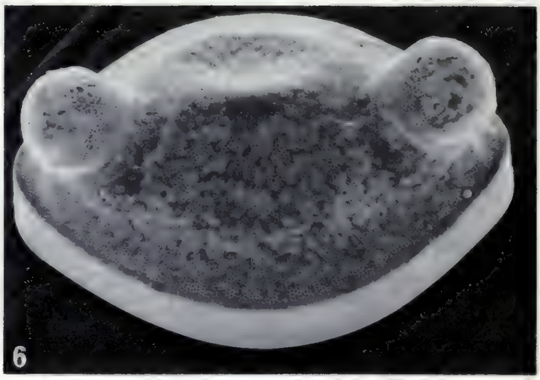
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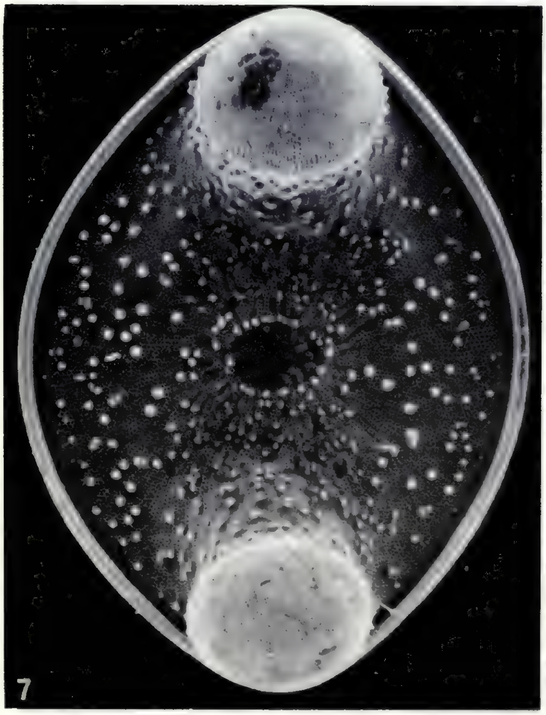
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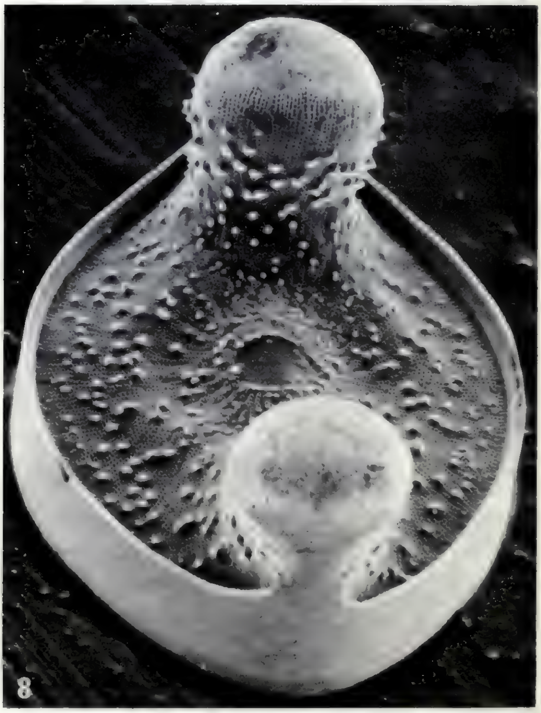
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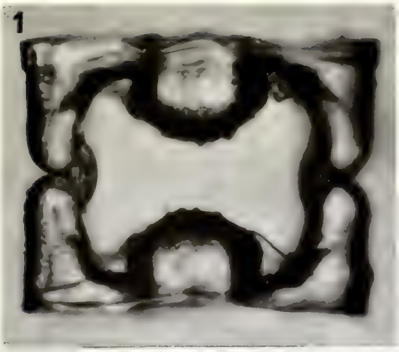

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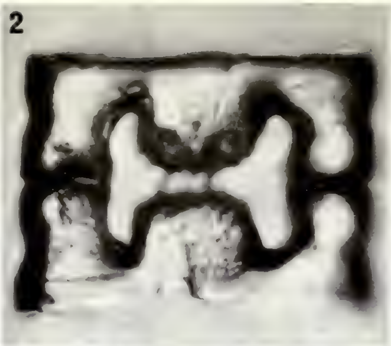

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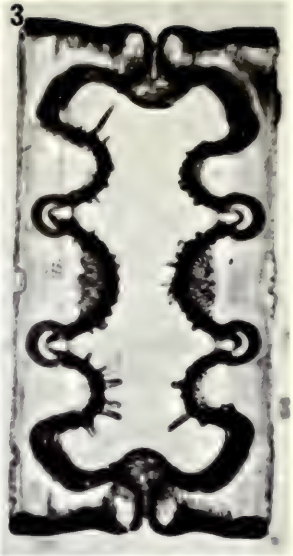

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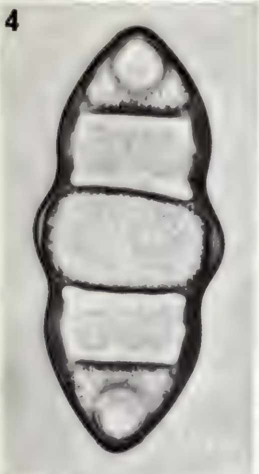

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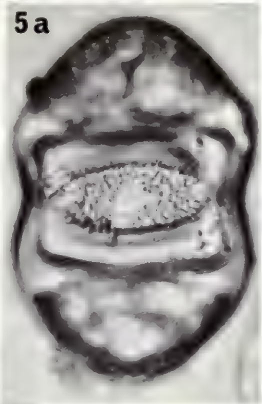

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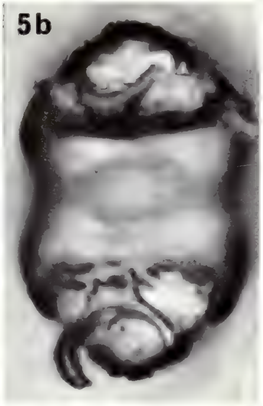

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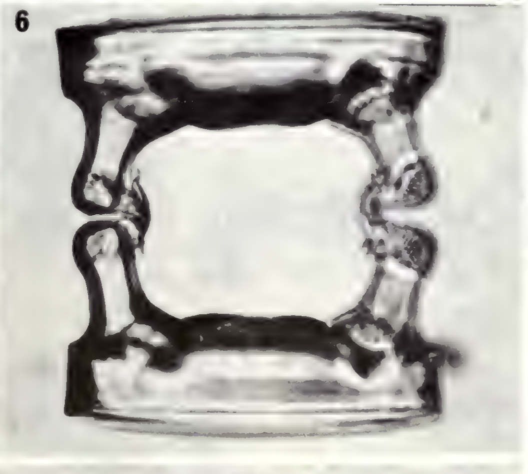

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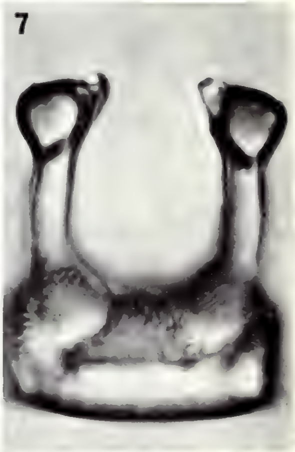

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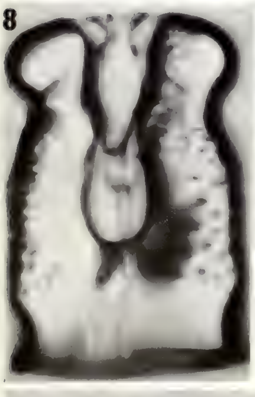

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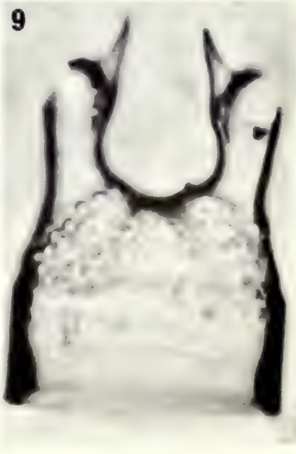

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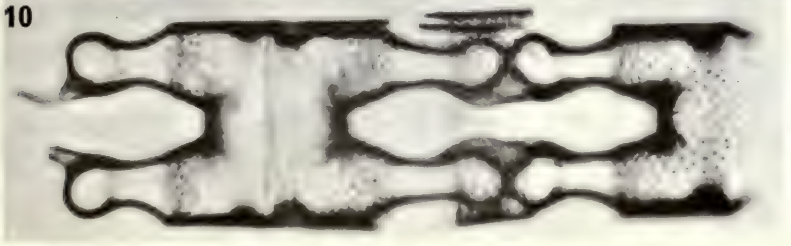

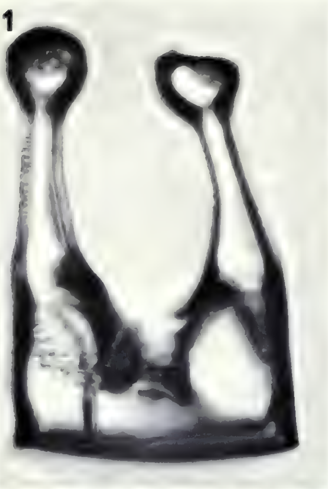

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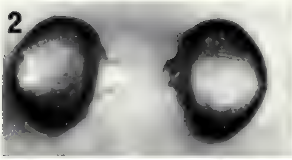

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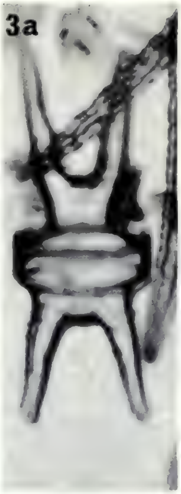

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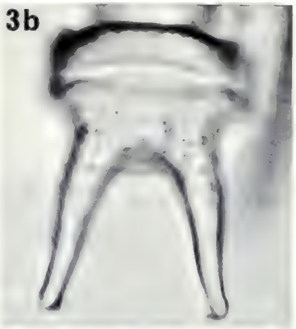

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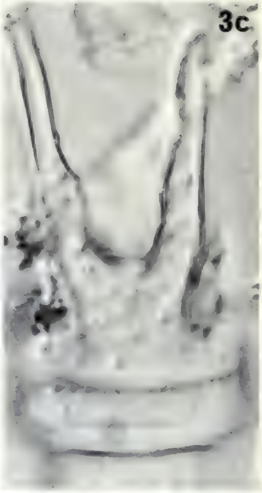

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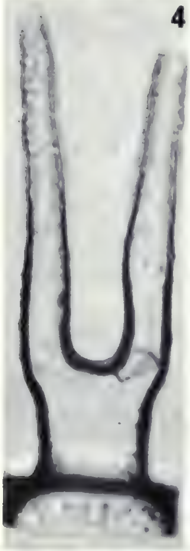

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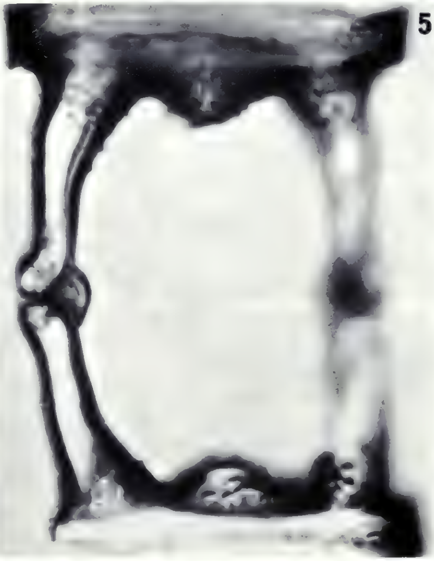

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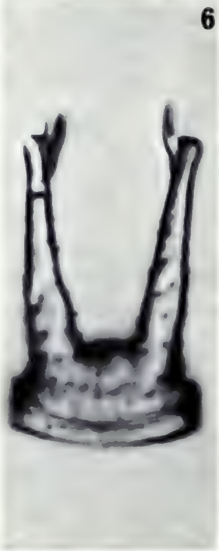

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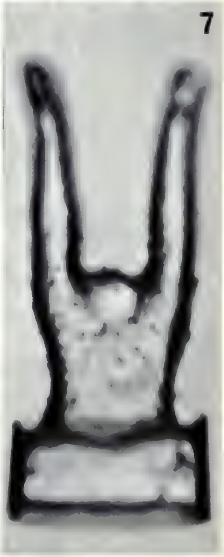

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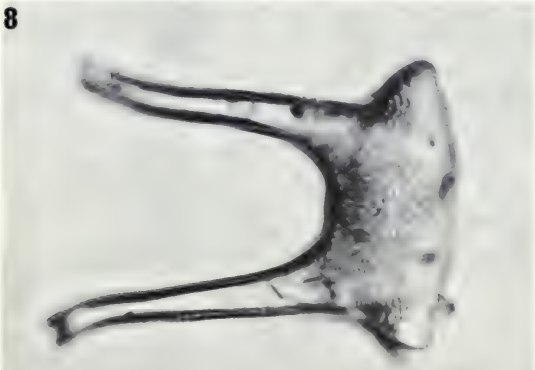

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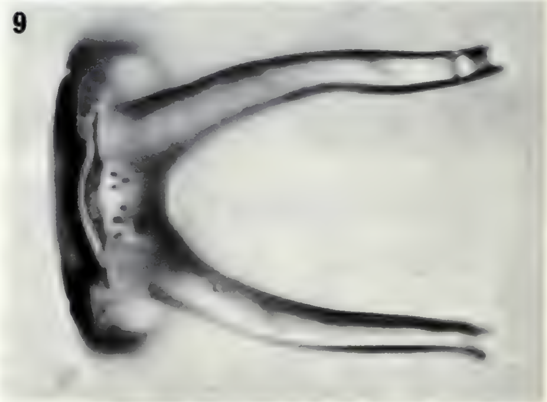

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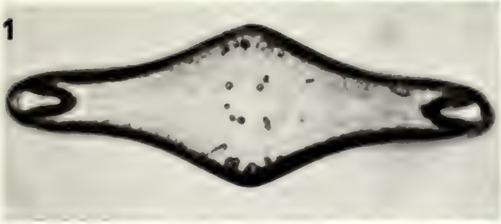
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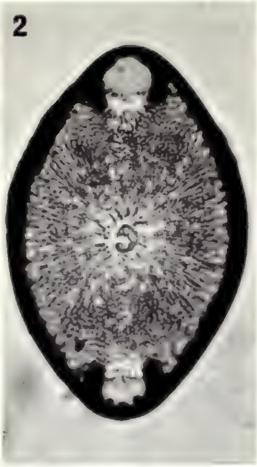
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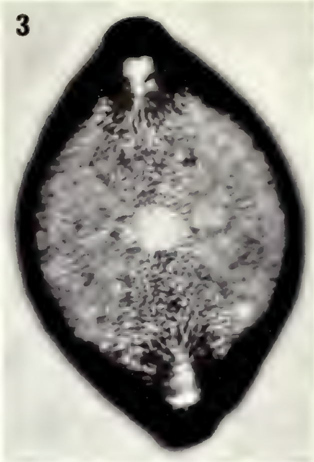
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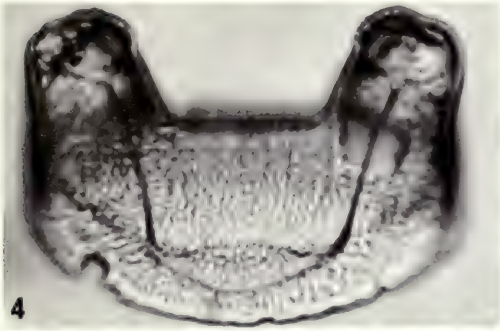
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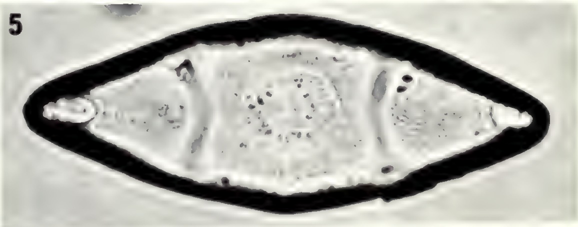
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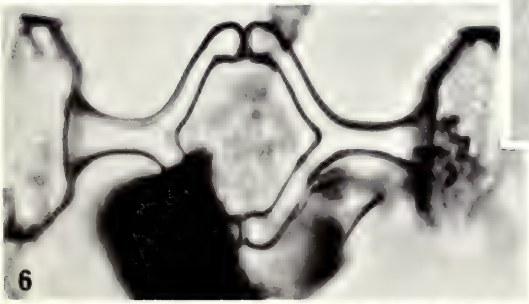
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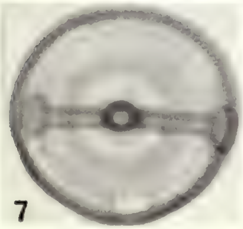
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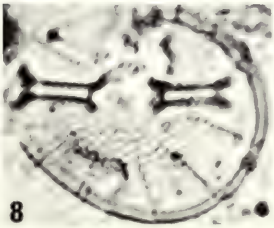
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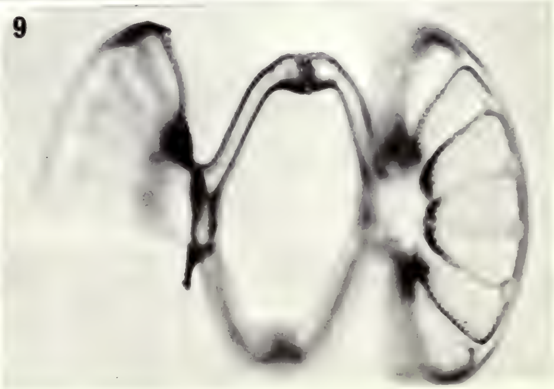
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British Museum (Natural History)

Ferns of Jamaica
A guide to the Pteridophytes

G. R. Proctor

This flora records and describes the 579 species and 30 varieties of ferns occurring in Jamaica. The succinct species descriptions include relevant synonymy and incorporate distributional data both within and outside Jamaica. Special emphasis is given to the subtle distinctions between closely related species and all genera are illustrated. Keys to the genera and species facilitate a wider use of the flora in the West Indies and northern South America. The author, one time Senior Botanist in charge of the Herbarium of the Science Museum, Kingston, Jamaica, is an outstanding field botanist and his expertise is reflected in the practicality of the flora and especially in the habitat and ecological information. This volume represents an important addition to our knowledge of the flora of the West Indies.

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